

FRUITS AND SEEDS OF THE BRANDON LIGNITE, VI.
MICRODIPTERA (LYTHRACEAE)

BRUCE H. TIFFNEY

THE BRANDON LIGNITE is a small deposit of brown coal and associated sediments of presumed Oligocene age in Forestdale, Vermont (lat. 43°50' N., long. 73°03' W.). It contains a rich flora and has been the focus of much research, including the present investigation of fruits and seeds. For a review of the history and geology of the site, see Tiffney (1977, 1979, 1980a) and Tiffney and Barghoorn (1976, 1979).

The specimens are compactions—three dimensional and retaining much of their original organic matter. They were recovered by disaggregating the matrix in either sodium carbonate or dilute hydrogen peroxide and sieving the resulting sediment for the small organic fraction. This was examined under a dissecting microscope, and the seeds were picked out with a fine brush. Specimens were stored in a 1:1 solution of glycerine and 50 percent alcohol. Sectioned material was embedded in paraffin by standard methods and cut at 10 μ m. intervals. Whole specimens were photographed with a Nikon SMZ-10 dissecting microscope with a Nikon PFM photographic attachment; sectioned material with a Leitz Ortholux compound microscope equipped with the same photographic attachment. Scanning electron micrographs were made with a Perkin-Elmer ETEC U-1 Autoscan. Modern material of *Decodon* was obtained from herbarium specimens in the Gray (GH) and Arnold Arboretum (A) Herbaria of Harvard University.

GENERAL SURVEY OF THE FOSSIL FRUITS
AND SEEDS OF THE LYTHRACEAE

The Lythraceae is a cosmopolitan, predominantly tropical family of 22 to 25 genera and 450 to 550 species of herbs, shrubs, and trees (Engler, 1964; Willis, 1973; Heywood, 1978). Many of the herbs are aquatics, and other members of the family commonly inhabit damp ground (Graham, 1964). The shrubs and trees include both evergreen and deciduous members. The family is well represented in the fossil record by fruits and seeds. General reviews of the fossil history of the group have been provided by Sahni (1943), Graham and Graham (1971), and Eyde (1972). Two tribes are recognized in the modern family, based on the completeness of septation of the capsule (Koehne, 1903; Engler, 1964): in the Lythraeae septation is not complete to the apex, while in the Nesaeae it is. This character, however, is often difficult to apply (Graham, 1964).

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Many of the fossils cannot be ascribed to one section or the other because they are too poorly preserved. These include *Cranmeria trilocularis* Reid & Chandler (Chandler, 1961a), *Pachyspermum quinqueloculare* Reid & Chandler (Reid & Chandler, 1933), *Tamesicarpum polyspermum* Reid & Chandler (Chandler, 1961a), all from the latest Paleocene and Early Eocene of southern England, and *Enigmocarpon parijai* Sahni (Sahni, 1943) from the Paleogene Deccan Intertrappean series of India.

Ammannia lakensis Chandler (Chandler, 1962), from the Lower Eocene of southern England, is the oldest known representative of the Lythraeae. *Palaeolythrum bournense* Chandler has been reported from Middle Eocene sediments in southern England, and *P. gailense* Chandler from the Pliocene of France (Chandler, 1963b). *Lythrum* L. is known from the Japanese Pliocene (Miki, 1959).

Nesaeae are also first recognized in the Early (*Alatospermum lakense* Chandler; Chandler, 1962) and Middle (*Ministerocarpum alatum* Reid & Chandler; Reid & Chandler, 1933) Eocene of southern England, and *Lagerstroemia indica* L. is known from the Pliocene of Japan (Miki, 1937). Mai (1960, 1964) reported two species of *Lagerstroemia*, *L. lignitum* (Menzel) Mai and *L. europaea* Mai, from Miocene sediments in Germany. Subsequent investigation resulted in the transfer of both species to *Polyspora* Sweet (= *Gordonia* Ellis; Theaceae) (Mai, 1971; Gregor, 1978a, 1978b). The seeds of *Decodon* J. F. Gmelin, *Microdiptera* Chandler, and *Mneme* Eyde, together with those of *Alatospermum*, comprise a morphological complex to which the Brandon fossils belong. This necessitates a review of the systematic history, morphological characters, and geologic distribution of these genera in order to place the Brandon specimens in context.

FOSSIL RECORD OF DECODON AND RELATED TAXA

C. and E. M. Reid (1907) illustrated (but did not describe) an unidentified seed from the Pliocene of Tegelen, The Netherlands. This seed was subsequently reported from Raevens, Belgium (C. & E. M. Reid, 1908), and from Reuver, The Netherlands (C. & E. M. Reid, 1915), both of Pliocene age. In the last publication, the fossil was compared to *Stocksia* Benthams (Sapindaceae). A closely allied species was then found from the Pliocene of France. In 1920 E. M. Reid indicated that these specimens could not be compared to *Stocksia* and then proposed *Diclidocarya*, in which she included *D. gibbosa* (E. M. Reid, 1920) and *D. globosa* (E. M. Reid, 1923), from Pliocene sediments of western Europe and Russia, and *D. menzelii* (E. M. Reid, 1927), from the Oligocene of Germany. The familial affinities of the genus were regarded as uncertain, although the species were considered to be aquatics (E. M. Reid, 1920).

P. A. Nikitin (1929) recognized that the morphology of these seeds matched that of the extant monotypic *Decodon* of eastern North America and transferred *Diclidocarya globosa* to *Decodon globosus* (E. M. Reid) P. A. Nikitin. E. M. Reid (1929), in an article appended to Nikitin's, agreed to this identification and extended it to include the type species of *Diclidocarya*, *D. gibbosa*, which became *Decodon gibbosus* (E. M. Reid) E. M. Reid. However, Reid's

analysis indicated that *Diclidocarya menzelii* was distinct from *Decodon* at the generic level, and she retained *D. menzelii* without providing a new generic name in place of *Diclidocarya*, now a synonym of *Decodon*. Eyde (1972) resolved this problem by providing the name *Mneme*. Chandler (1957) established a third genus of related fossil seeds, *Microdiptera* Chandler.

Decodon. Thirteen species of *Decodon* are presently recognized (*D. tetraedri-formis* Raniecka-Bobrowska (Raniecka-Bobrowska, 1957) has been recognized as a synonym of *D. globosus* (Dorofeev, 1963a; Friis, 1980)). The majority of these species, as well as most of the individual reports, are from Siberia, but the genus was also widespread in western Europe. The number of species was low in the Eocene (one), increased in the Oligocene (five), peaked in the Miocene (ten), and shrank in the Pliocene (four), leading to the single extant species. The genus is of sufficient interest to have warranted reviews by Raniecka-Bobrowska (1957) and Dorofeev (1977a), the latter including the description of nine new species from the U.S.S.R. Two incomplete maps of fossil distributions have been published (Dorofeev, 1963c; Palamarev, 1970). A reasonably complete enumeration of the reported fossils is given in TABLE 1.

The seeds of *Decodon* are anatropous and bitegmic and are borne about 20 to 30 per 3- or 4-loculed capsule of approximately 5–6 mm. diameter. Because the seeds are tightly packed within the fruit, they are generally elongate-pyramidal (PLATE I, A, C), with sharply rounded or angular corners and no clear lateral wings. There is a wide variation in shape due to degree of locular compression and stage of development. The seeds vary between 0.8 and 1.9 mm. in length (average, 1.2 mm.) and 0.6 and 1.9 mm. in width/thickness (average, 0.98 mm.). The raphe commences at the apical point beneath the micropyle and runs through the dorsal¹ face to the base

¹There is some confusion in distinguishing the dorsal and ventral faces. E. M. Reid (1920; also 1927, 1929), in establishing *Diclidocarya* (= *Mneme*), considered the germination valve to be on the ventral face and the raphe crest to be on the dorsal. This usage has been followed by many subsequent authors (e.g., Kirchheimer, 1957; Mai & Walther, 1978; Friis, 1980) in descriptions of *Decodon*, *Mneme*, and *Microdiptera*. Chandler followed this convention in describing *Decodon gibbosus* (1960) and *D. vectensis* Chandler (Chandler, 1963a). However, in describing *Microdiptera parva* Chandler (Chandler, 1957, 1961b, 1963a), *Mneme minor* Chandler (Chandler, 1960), and *Alatospermum lakense* Chandler (Chandler, 1963b), she considered the germination valve to be on the dorsal face, a distinction also followed by Mai (1964) for *Microdiptera parva* and Holý (1976) for *Mneme donata*.

The question of correct interpretation can be determined only from the relationship of the seeds to the fruit axis. Fossil fruits are known in two cases. That reported by Holý (1976) is not described in detail. In *Microdiptera major* Chandler (Chandler, 1963b) the seeds are packed in tightly overlapping longitudinal rows, with their flat faces parallel to the long axis of the fruit, the individual seeds radiating in a "starburst" from the central columella. The same relationship is seen in the fruits of modern *Decodon*. As a result, a logical distinction between dorsal and ventral faces cannot be made, and a choice between the two becomes arbitrary. Indeed, the distinction is perhaps completely unwarranted, but its use is so entrenched in the literature that its rejection would confuse, rather than clarify, matters. This paper follows E. M. Reid's original usage in treating the germination valve as ventral and the raphe as dorsal. Discovery of new fossil fruits may modify this conclusion.

TABLE 1. Reported Taxa of *Decodon*.

Taxon	Age	Locality	Citation
Sect. GIBBOSUS Dorofeev			
<i>Decodon gibbosus</i> (E. M. Reid) E. M. Reid			
f. <i>gibbosus</i> , f. <i>elongatus</i> Dorofeev	Late Eocene	Barton Beds, England	Chandler, 1960
	Oligocene?	Svetlogorsk, Lithuania	Dorofeev, 1963b
	Oligocene	W. Siberia, USSR (9 localities)	Dorofeev, 1963a
	Oligocene	Tara, W. Siberia, USSR	Dorofeev, 1957a
	Oligocene	Beloyarka, Transuralia, USSR	Dorofeev, 1968
	Early Miocene	Lagernogo Sada, Tomsk, W. Siberia, USSR	P. A. Nikitin, 1965
	Miocene	Rostov, Ukraine, USSR	Dorofeev, 1959b
	Miocene	W. Siberia, USSR (9 localities)	Dorofeev, 1963a
	Miocene	Mammoth Mt., W. Siberia, USSR	Dorofeev, 1969
	Miocene?	Bashkiria, S. Urals, USSR	Kolesnikova, 1960
	Mid Miocene	Fasterholt, Denmark	Friis, 1980
	Mid/Late Miocene	Irtys R., W. Siberia, USSR	Dorofeev, 1959a
	Late Miocene	Odessa, Ukraine, USSR	Dorofeev, 1951
	Late Miocene	Odessa, Ukraine, USSR	Dorofeev, 1955b, 1955e
	Late Miocene	NE. Moldavia, USSR	Negru, 1972
	Late Miocene	SW. Moldavia, USSR (6 localities)	Negru, 1979
	Pliocene	Bug R., Tiligul R., W. Siberia, USSR	Dorofeev, 1955d

	Pliocene	Pont de Gail, France	E. M. Reid, 1920
Sect. GLOBOSUS Dorofeev			
<i>D. aldanensis</i> Dorofeev	Miocene	Mammoth Mt., W. Siberia, USSR	Dorofeev, 1977a
<i>D. bashkiricus</i> Dorofeev	Pliocene	Bashkiria, S. Ural Mts., USSR	Dorofeev, 1977a
<i>D. europaeus</i> Dorofeev	Miocene	Tambov region, Russia, USSR	Dorofeev, 1977a
<i>D. globosus</i> (E. M. Reid) P. A. Nikitin	Oligocene	Tara, W. Siberia, USSR	Dorofeev, 1957a
	Early Miocene	Lagernogo Sada, Tomsk, W. Siberia, USSR	P. A. Nikitin, 1965
	Miocene	Mammoth Mt., W. Siberia, USSR	Dorofeev, 1969
	Miocene	Rostov, Ukraine, USSR	Dorofeev, 1959b
	Miocene	W. Siberia, USSR (6 localities)	Dorofeev, 1963a
	Miocene	Stare Gliwice, Poland	Szafer, 1961
	Mid/Late Miocene	Irtys R., W. Siberia, USSR	Dorofeev, 1959a
	Late Miocene	NE. Moldavia, USSR	Negru, 1972
	Late Miocene	Vienna Basin, Austria	Knobloch, 1976a
	Late Miocene	Bug R., Tiligul R., W. Siberia, USSR	Dorofeev, 1955d
	Late Miocene	Odessa, Ukraine, USSR	Dorofeev, 1955b, 1955e
	Late Miocene	Konin, central Poland	Raniecka-Bobrowska, 1959
	Late Miocene	SW. Moldavia, USSR (5 localities)	Negru, 1979
	Miocene/Pliocene	Domajski Wierch, Poland	Szafer, 1952
	Pliocene	Tegelen, Netherlands	E. M. Reid, 1927
	Pliocene	Raevels, Belgium	E. M. Reid, 1927
	Pliocene	Reuver, Netherlands	E. M. Reid, 1927
	Pliocene	Bashkiria, Russia, USSR	Dorofeev, 1960

TABLE 1 (continued).

Taxon	Age	Locality	Citation
<i>D. globosus</i> (E. M. Reid)	Pliocene	Bashkiria, Russia, USSR	Dorofeev, 1977b
P. A. Nikitin (cont'd.)	Pliocene	Kama R., Ural Mts., USSR	Dorofeev, 1957b
	Pliocene	Matanov Garden, S. Russia, USSR	Dorofeev, 1966
	Pliocene	Baldevo, SW. Bulgaria	Palamarev, 1970
	Pliocene	Pont de Gail, France	Reid, 1923
<i>D. maeoticus</i> Dorofeev	Late Miocene	Odessa, Ukraine, USSR	Dorofeev, 1977a
<i>D. nikitinii</i> Dorofeev	Miocene	Lezhanka, W. Siberia, USSR	Dorofeev, 1977a
<i>D. sibiricus</i> Dorofeev	Oligocene	W. Siberia, USSR (4 localities)	Dorofeev, 1963a (see also Dorofeev, 1962)
	Oligocene	Beloyarka, Transuralia, USSR	Dorofeev, 1968
	Early/Mid Miocene	Polevskoi, Ural Mts., USSR	Dorofeev, 1970
	Miocene	W. Siberia, USSR (7 localities)	Dorofeev, 1963a (see also Dorofeev, 1962)
	Miocene	Mammoth Mt., W. Siberia, USSR	Dorofeev, 1969
<i>D. sphenosus</i> G. Bal.	Unknown	W. Siberia, USSR	V. P. Nikitin, 1968
<i>D. tanaiticus</i> Dorofeev	Pliocene	Krivobor'e, Ukraine, USSR	Dorofeev, 1977a
Sect. VECTENSIS Dorofeev			
<i>D. antiquus</i> Dorofeev	Miocene	Tambor region, Ural Mts., USSR	Dorofeev, 1977a
<i>D. tavidensis</i> Dorofeev	Oligocene	Sverdlovsk region, Ural Mts., USSR	Dorofeev, 1977a
	Mid Miocene	Fasterholt, Denmark	Friis, 1980
<i>D. vectensis</i> Chandler	Oligocene	Isle of Wight, England	Chandler, 1963a
	Oligocene	Beloyarka, Transuralia, USSR	Dorofeev, 1968
	Mid Miocene	Fasterholt, Denmark	Friis, 1980

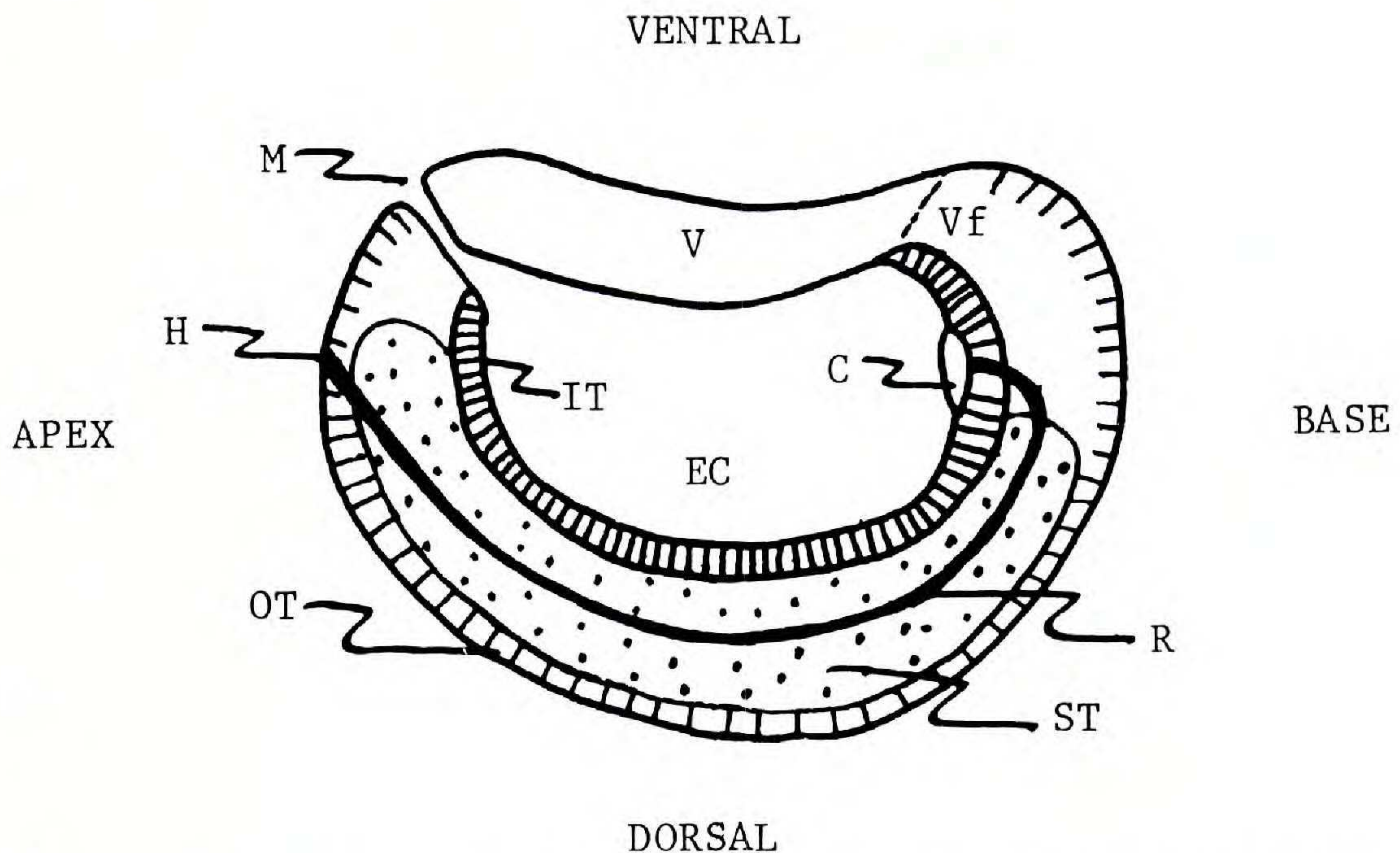


FIGURE 1. *Decodon verticillatus*, longitudinal section (after P. A. Nikitin, 1929). V = valve, Vf = valve flexure, C = chalaza, IT = crystal-bearing inner testa, EC = embryo cavity, R = raphe, ST = spongy tissue, OT = outer testa, H = hilum, M = micropyle.

of the seed, where it enters the obovoid embryo cavity via the expanded chalaza (see FIGURE 1; PLATE I, B). There are no furrows on the dorsal face. The oblong, slightly concave germination valve occupies one half to three quarters of the width of the ventral face, and one half to three quarters of its length (PLATE I, A). The surface of the valve is marked by six to twelve longitudinal rows of small pits that are 30–40 μm . in diameter. In modern seeds this detail is largely obscured by the thick epidermal coat. At maturity, the valve separates from the central body along its apical and lateral margins, pivoting on its attached base, and thus exposes the ellipsoid embryo cavity. The micropyle is situated at the apex of the seed, between the tip of the germination valve and the hilar scar (PLATE I, B). The structure of the outer integument is complicated (PLATE III, D). The outermost stratum is 14–52 μm . thick and is formed of one or two layers of large, elongate to equidimensional (14–36 \times 21–52 μm .) epidermal cells with dark contents. This expands to eight to ten cells in thickness over the concave germination valve, making the seed surface in this area appear flat or slightly convex. There is some tendency for the epidermis to thicken over the two basal corners of the seed. Beneath the epidermis is an attenuated (15–21 μm .) outer sclerotesta of one or two equiaxial to elongate sclereids, 10–18 \times 18–30 μm . in size; this layer thickens beneath the germination valve and there becomes contiguous with the inner sclerotestal wall surrounding the embryo cavity. The inner sclerotesta is approximately 45–75 μm . thick and consists of five to seven layers of irregularly shaped, small (17–41 μm .), thick-walled

cells that frequently contain octahedral crystals in their lumina. Where the outer testa abuts the germination valve, the delimiting cells become palisadelike and function as the zone of weakness along which the valve opens (P. A. Nikitin, 1929; see PLATE II, C, D for a similar structure in *Microdiptera*). Between the outer and inner sclerotestae on the dorsal and (to some degree) lateral faces is an intermediate layer of isodiametric spongy parenchyma cells 12–33 μm . in diameter, which presumably aid in flotation dispersal of the seed. When seen three dimensionally, this tissue forms a bowl that cups the embryo cavity and has a dip in its margin beneath the germination valve. The raphe occupies a tunnel curving through this spongy layer from apex to base (FIGURE 1; PLATE III, D). The inner integument is formed of a single layer of elongate (9–18 \times 50–105 μm .) cells sheathing the embryo cavity.

Dorofeev (1977a; see also Friis, 1980) recognizes three morphological species groups in *Decodon*. The gibbosus group includes one species, *D. gibbosus* (33 reports), which ranges from Late Eocene to Pliocene. The seeds have narrow ventral faces, rounded edges, and well-developed dorsal tissue (FIGURE 2, a). Dorofeev (1955e) further divided this group into two forms: f. *gibbosus*, characterized by wedge-shaped seeds with moderately developed dorsal spongy tissue; and f. *elongatus*, in which the dorsal spongy tissue is strongly developed. No published report exists of the relative thicknesses of the internal and external sclerotestal walls of the dorsal face in the gibbosus group. The globosus group includes *D. aldanensis* Dorofeev, *D. bashkiricus* Dorofeev, *D. europaeus* Dorofeev, *D. globosus* (E. M. Reid) P. A. Nikitin, *D. maeoticus* Dorofeev, *D. nikitinii* Dorofeev, *D. sibiricus* Dorofeev, *D. tanaiticus* Dorofeev, and the living species *D. verticillatus* (L.) Ell. (48 reports) and ranges from the Oligocene to the present. One further member of the

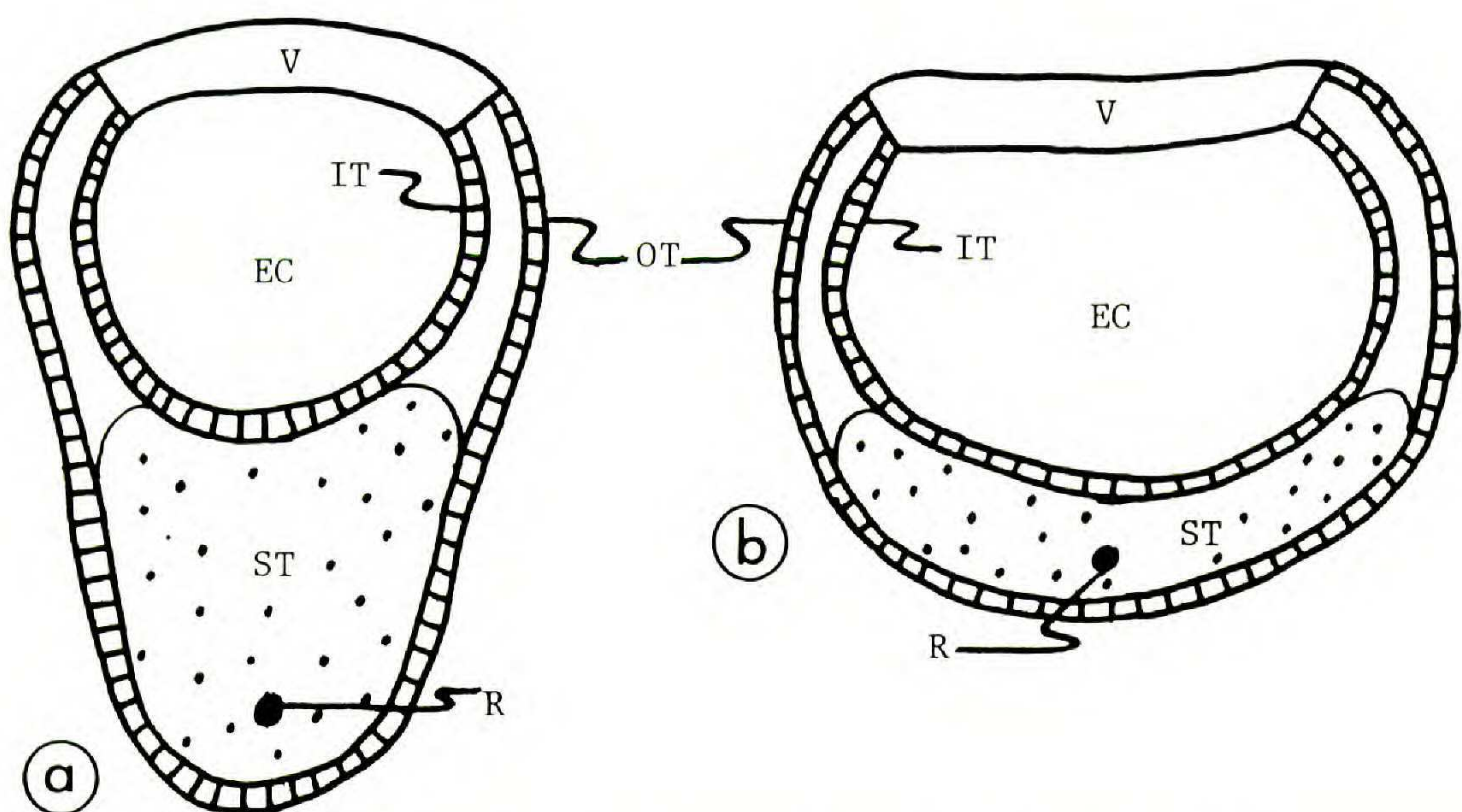


FIGURE 2. Cross sections: a, *Decodon gibbosus*; b, *D. globosus*. Conventions as in Figure 1.

group, *D. sphenosus* G. Bal., is potentially unique morphologically; however, this name is a *nomen nudum* since it was not validly published. Seeds of the globosus group have broad ventral faces, rounded edges, poorly developed dorsal spongy tissue (FIGURE 2, b), and a germination valve extending almost the full length of the ventral face. P. A. Nikitin (1929) noted that the lateral margins of *D. globosus* are convex to straight and that the external sclerotesta of the dorsal face is thicker than the inner, in contrast to *D. verticillatus*, which has straight to concave lateral margins and a thin external and thick internal sclerotesta. The vectensis group includes *D. antiquus* Dorofeev, *D. tavidensis* Dorofeev, and *D. vectensis* Chandler (six reports), ranging from Oligocene to Middle Miocene. Seeds of this group are characterized by a narrow ventral face, sharply angled edges, weak development of the dorsal spongy tissue, and a germination valve that extends most of the length of the ventral face. In *D. vectensis* the inner dorsal sclerotestal wall is thicker than the outer (Chandler, 1963a).

The only absolute character of apparent value in *Decodon* is the thickness of the inner and outer sclerotestae, although data on this are limited. In *D. verticillatus* and *D. vectensis* the outer testa is thinner than the inner, while in *D. globosus* the outer is thicker than the inner. This author is not aware that the character has been reported for other species. Beyond this, species delimitation is based on size and shape—both characters of continuous variation. None of the size distinctions between species is supported by statistical analysis, and the narrow range of seed size (0.5–1.9 mm.) in the genus, together with the complete overlap of species size ranges, suggests that the character is of little value, an opinion already expressed by Chandler (1960). Shape is little better. Some of the more elongate forms (e.g., *D. tavidensis*, *D. antiquus*) are distinctive, but these overlap in morphology both with each other and with more angular specimens of other species. *Decodon gibbosus* and *D. globosus* are classically separated by the greater development of dorsal spongy tissue in the former (FIGURE 2), but this also may simply be a gradational feature of no taxonomic importance. Mai (Mai *et al.*, 1963) suggested that *D. gibbosus* and *D. globosus* were but extremes of a continuum and subsequently (Mai & Walther, 1978) reduced the two to one species, *D. gibbosus*, with two subsidiary groups corresponding to *D. gibbosus* and *D. globosus*. He further suggested that the species of Dorofeev (1977a) were but forms within these groups. In the absence of an examination of all the fossil forms, this cannot be conclusively proved, but the present author is in full agreement with Mai's opinion.

Mneme. The seeds of *Mneme* are anatropous and bitegmic. At least in *M. menzelii* (E. M. Reid) Eyde, the 30 to 40 seeds were borne in a 4- to 6-locular capsule (Kirchheimer, 1957). The seeds are generally flattened and subcircular to oval in face view, with the ventral surface convex and the dorsal flat to convex. The central embryo cavity is normally flanked by two clear "wings," although these are nearly absent in some species of *M. sibirica* (P. A. Nikitin) Eyde, which is quite variable in shape. In a specimen of *M. menzelii* from Frecheu, West Germany, studied and illustrated here (PLATE III, A, B),

the wings are particularly clear, perhaps partly due to compression. The relative lack of variability in published specimens of *M. menzelii*, in contrast to those of *M. sibirica*, may involve the degree of packing of seeds in the capsule. The seeds of *Mneme* generally range from 1 to 2.5 mm. (average, 1.5 mm.) in length, and from 1 to 2.4 mm. (average, 1.4 mm.) in width. *Mneme minor* (Chandler) Eyde has much smaller (0.75–0.85 × 0.8–0.95 mm.) seeds. The raphe runs from the apical hilum along the dorsal testa to the basal chalaza; the lateral localization of spongy tissue dictates that the raphe is nearer the seed surface than in *Decodon*. The path of the raphe is generally flanked by two deep, narrow depressions (Friis, 1980; FIGURE 4, a), which extend about three quarters of the length of the seed and separate the wings from the body. These are nearly absent in *M. donata* Holý (Holý, 1976). Friis (1980) indicates that the central body is fully embedded in the wing tissue in *Mneme*. The elongate-elliptic germination valve fills one quarter to one third the width and one half to two thirds the length of the ventral face, although in *M. sibirica* it can occupy one sixth to four fifths the width due to overall variability in seed shape. In the specimen of *M. menzelii* from Frecheu (PLATE III, A) and in specimens examined by Friis (1980), the surface of the cap is lined by approximately twenty parallel rows of small pits. However, in seeds of this species illustrated by Knobloch (1976b, pl. 1, fig. 18) and in drawings of this species provided by Dorofeev (1969, fig. 35), six to nine rows of pits seem to be present. In *M. donata* the valve has eight rows of pits. The valve detaches completely from the testa to reveal the ellipsoid embryo cavity, which runs the full length of the seed. The micropyle is ventral to the hilum on the apical terminus, just beneath the termination of the valve. The seed is surrounded by a thick, dark epidermal layer (E. M. Reid, 1927). The outer integument forms a strong testa of radially elongate sclereids around the seed body but is differentiated into three layers on the lateral wings. Here an intermediate layer of spongy, isodiametric, 6–12 μm . cells with pitted walls (Friis, 1980) is developed. This is bounded to the exterior by a 35–45 μm . thick outer sclerotesta (measurements from Frecheu specimen) and to the interior by the lateral walls of the “inner” sclerotesta around the seed body. In specimens of *M. menzelii* from Senftenberg (E. M. Reid, 1927) the outer sclerotesta is thinner than the inner. The outer and inner sclerotestae unite on the ventral and dorsal surfaces of the central body. The sclerotesta thins beneath the germination valve, where it is apparently rich in crystalline inclusions in the cell lumina (Friis, 1980). The inner integument is formed of thin cells 50–60 μm . long and 6 μm . wide. This summary is based on published material and on a specimen of *M. menzelii* from Frecheu, West Germany, that is now in the Paleobotanical Collections of the Botanical Museum, Harvard University (#51392).

With the exception of two reports (*Mneme* sp. (Dorofeev, 1963a, 1969) and *M. triangulata* G. Bal. (V. P. Nikitin, 1968; possibly a *nomen nudum*)) for which full information is not available, there are three species. *Mneme menzelii* (27 reports) is the most common, ranging from (?Oligocene) Miocene to Pliocene and from Siberia to west-central Europe. It is primarily distinguished by the moderate to strong development of the lateral wings, and

by the indistinct separation of the wings from the central body. The latter feature may be a function of the inflated nature of the wings (FIGURE 4, a). *Mneme sibirica* is known from eight localities of Oligocene to Miocene age in western Siberia. It is highly variable in morphology (e.g., P. A. Nikitin, 1965, *pl. 14, figs. 1-3*) and is separated only with difficulty from *M. menzelii*. *Mneme minor* is the oldest; it is known from one report from the Late Eocene of southern England. It is distinguished by its small size and by the clear separation between the wing and the body. *Mneme donata* was described by Holý from Miocene sediments in Czechoslovakia. Its characters are closer to those of *Microdiptera*, to which it is here transferred. A summary of published reports is given in TABLE 2.

Microdiptera. The seeds of *Microdiptera* are generally similar to those of *Mneme*. They are anatropous and bitegmic and were borne in a multilocular, presumably capsular, fruit (Chandler, 1963b). The seeds tend to be dorsiventrally flattened, with the ventral surface convex and the dorsal concave to flat. The shape is irregularly obtriangular, varying from small and elongate to larger and broader forms. The corners are generally rounded but may be sharply angled in *M. major* Chandler and *M. uralensis* (Dorofeev) Friis. (The latter name is here used in a provisional sense—it is a *nomen nudum* since it has not been formally published.) Although the lateral wings are generally large and flat, they are sometimes narrow (e.g., *M. elongata* (Dorofeev) Dorofeev, *M. uralensis*, and some specimens of *M. parva* Chandler). The seeds range from 0.9 to 2 mm. (average, 1.25 mm.) in length, and 0.5 to 2 mm. (average, 1.26 mm.) in width. The path of the raphe follows the dorsal side of the seed body as in *Mneme*, and it is flanked by two depressions that extend nearly the full length of the seed and separate the wings from the seed body (PLATE II, F; FIGURE 3, b). Friis (1980) suggests that these grooves are shallow (FIGURE 4, b), although in some illustrated specimens of *M. parva* (e.g., Chandler, 1963a), *M. major* (Chandler, 1963b, *pl. 19, figs. 9, 13*), *M. uralensis* (Dorofeev, 1970, *fig. 12*), and the Brandon specimens (PLATE II, F) they appear to be deep. Friis (1980) describes the central body as being only partially embedded in the wing tissue, protruding about half of its diameter above the ventral face of the wing (FIGURE 4, b). The convex, oval to elliptic germination valve occupies between one quarter and one half the width of the ventral face (PLATES I, D-F; II, A, B) and about half its length, although in one report of *M. parva* (Chandler, 1963a) it reaches about four fifths the length. The surface of the valve is traversed by five to eight (rarely to ten) longitudinal rows of equiaxial pits about 40–50 μm . in diameter (PLATE II, B). At maturity the valve falls off completely to expose the ellipsoid embryo cavity that stretches the full length of the seed. The micropyle is just beneath the apical terminus of the germination valve, ventral to the hilum. Only small remnants of the apparently thick cuticle have been observed (PLATE III, E, F), beneath which can be seen a thin layer of narrow (5–7 μm .), elongate (50–60 μm .) cells (PLATE II, C, E) that are particularly noticeable around the germination valve (Chandler, 1957, 1961b). The outer integument forms a lignified testa two or three cells

TABLE 2. Reported species of *Mneme*.

Species	Age	Locality	Citation
<i>Mneme donata</i> Holý	See <i>Microdiptera donata</i> (Holý)	Tiffney	
<i>M. menzelii</i> (E. M. Reid) Eyde	Oligocene?	Novonikol'skogo, W. Siberia, USSR	Dorofeev, 1955a
	Miocene	Senftenberg, E. Germany	E. M. Reid, 1927; Kirch- heimer, 1935, 1957
	Miocene	W. Siberia, USSR (5 localities)	Dorofeev, 1963a
	Miocene	Rostov region, USSR	Dorofeev, 1959b
	Miocene	Fasterholt, Denmark	Friis, 1980
	Miocene	Yakutsk, Siberia, USSR	Dorofeev, 1969
	Miocene	Rypin, Poland	Łańcucka-Środoniowa, 1957
	Miocene	S. Poland	Łańcucka-Środoniowa, 1963
	Miocene	Tomsk, Siberia, USSR	P. A. Nikitin, 1935
	Miocene?	Bashkiria, S. Ural Mts., USSR	Kolesnikova, 1960
	Mid Miocene	Wiesa bei Kamenz, E. Germany	Mai, 1964
	Mid Miocene	Lausitz, E. Germany	Mai, 1967
	Mid/Late Miocene	Irtys R., W. Siberia, USSR	Dorofeev, 1959a
	Late Miocene	Vienna Basin, Czechoslovakia	Knobloch, 1976a

	Late Miocene	S. Poland	Szafer, 1952
	Late Miocene	Konin, central Poland	Raniecka-Bobrowska, 1959
	Late Miocene	Kunovice, Moravia, Czechoslovakia	Knobloch, 1976b
	Late Miocene	Vienna Basin, Czechoslovakia	Čtyroký & Knobloch, 1976
	Miocene/Pliocene	Bol'shoi Yuksy, W. Siberia, USSR	Dorofeev, 1955c
	Pliocene	Razlog and Baldevo, SW. Bulgaria	Palamarev, 1970
	Pliocene	Ob R., Tomsk, W. Siberia, USSR	P. A. Nikitin, 1948
	Uncertain	W. Siberia, USSR	V. P. Nikitin, 1968
<i>M. minor</i> (Chandler) Eyde	Late Eocene	Barton Beds, England	Chandler, 1960
<i>M. sibirica</i> (P. A. Nikitin)	Oligocene	W. Siberia, USSR (6 localities)	Dorofeev, 1963a (see also Dorofeev, 1962)
Eyde	Early Miocene	Lagernogo Sada, Tomsk, W. Siberia, USSR	P. A. Nikitin, 1965
	Miocene	W. Siberia, USSR	Dorofeev, 1963a
<i>M. triangulata</i> G. Bal., <i>nomen nudum?</i>	Unknown	W. Siberia, USSR	V. P. Nikitin, 1968
<i>Mneme</i> sp.	Miocene	W. Siberia, USSR	Dorofeev, 1963a
	Mid/Late Miocene	Mammoth Mt., W. Siberia, USSR	Dorofeev, 1969

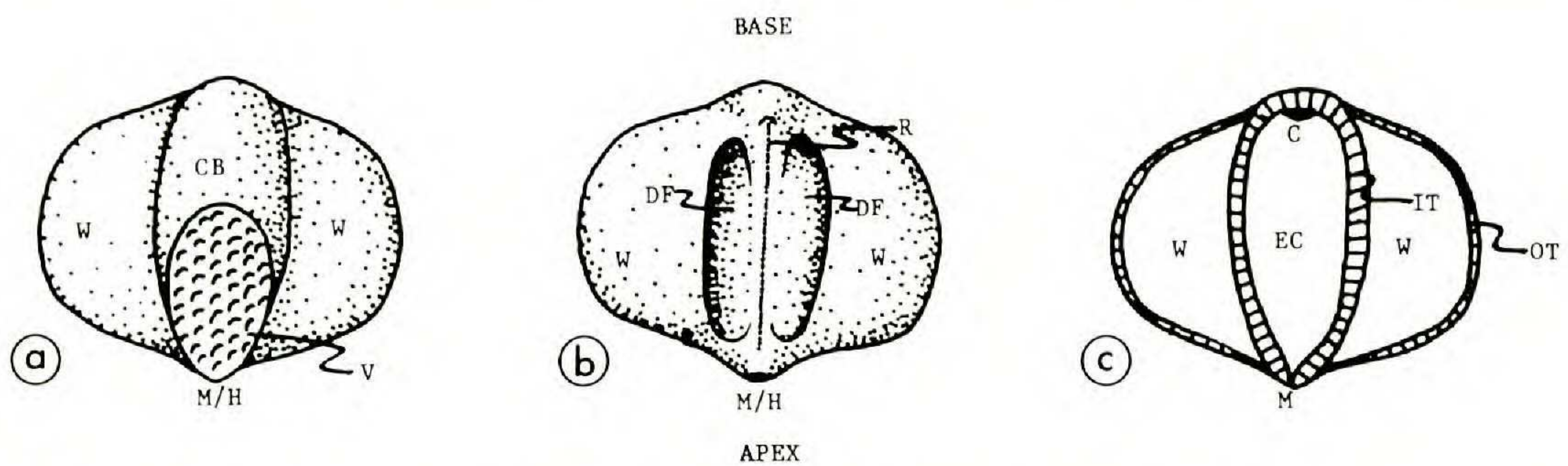


FIGURE 3. *Microdiptera parva*: a, ventral view; b, dorsal view. c, longitudinal section. CB = central body, W = wing, DF = dorsal furrow, other conventions as in FIGURE 1.

deep around the seed cavity. Near the germination valve it thickens and is formed of one to three layers of radially elongate sclereids, often with angular lumina indicating that crystals had once been present (PLATE III, H). Laterally, the outer integument is inflated by the intercalation of a zone of equiaxial spongy cells of 12–18 μm . diameter. This is bounded by a thin outer testa of one or two layers of weakly lignified small cells and the much thicker inner sclerotesta of the central body (FIGURES 3, c; 4, b). The inner integument is formed of elongate cells sheathing the inside of the embryo cavity. The foregoing description is based on published material and on the Brandon specimens.

There are six reported species of *Microdiptera*, although these can be reduced to two or perhaps even to one. The most common is *M. parva*, which is known from ten reports of Late Eocene to Middle Miocene age and, with the exception of the extension presented here, is restricted to western and central Europe. While *M. major* (Middle Eocene of southern England; one report) has distinctive mucrones on its apex and occasionally on its wing tips (e.g., Chandler, 1963b, *pl. 19, figs. 9–29*), similar features are sometimes seen in *M. parva* (Chandler, 1963a, *pl. 31, figs. 99–107*). Mai and Walther (1978) considered *M. major* to be a synonym of *M. parva*, noting that the two were separated by small characters that were seen to intergrade in large populations. *Microdiptera tavidensis* Dorofeev (Oligocene of the Urals; one report) is also quite similar to *M. parva*, and the present author concurs with Friis (1980) that the two likely represent a single species. *Microdiptera donata* (Holý) Tiffney (Miocene of Czechoslovakia; one report) was distinguished by Holý (1976) from specimens of *M. parva* that occurred in the same deposit. However, the morphology of *M. donata* overlaps with that of *M. parva* from Brandon, suggesting a degree of local variation in the latter species. Similarly, while *M. uralensis* (Miocene of the Urals; one report—a *nomen nudum*, see above) and *M. elongata* (Oligocene and Miocene of Siberia; three reports) are united by their narrow wings and elongate shape, both also overlap in morphology with the Brandon population of *M. parva*. An enumeration of the species in the literature is provided in TABLE 3, but it seems most likely that they may all be reduced to synonymy under *M. parva*, which may in turn ultimately be shown to be a species of *Mneme*.

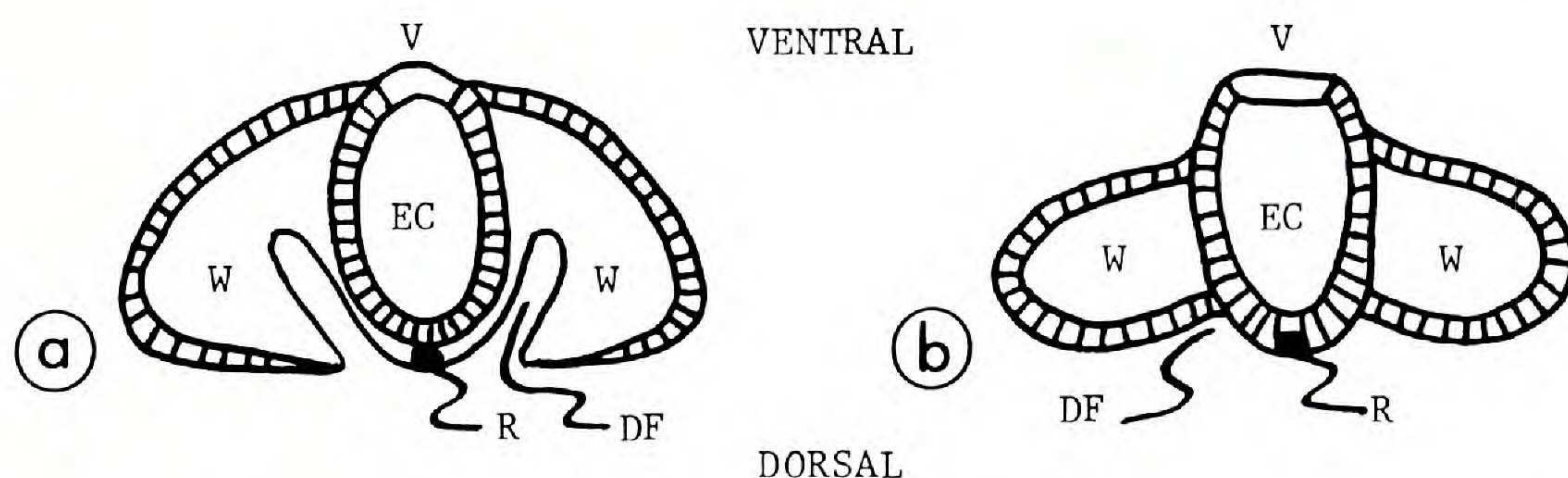


FIGURE 4. Cross sections (redrawn from Friis, 1980, with permission of author): a, *Mneme*; b, *Microdiptera*. Conventions as in Figures 1 and 3.

Alatospermum. The anatropous seeds of *Alatospermum* are similar to those of *Mneme* and *Microdiptera*; the fruit is not presently known. The seeds are dorsiventrally flattened and quite variable in shape, ranging from broadly triangular to nearly rectangular, often with a pointed apex and irregular lateral margins. The wings are completely lateral and are long, narrow, and thin; they are often missing or unequally developed on the two sides of the body. The seeds range from 0.75 to 1.55 mm. in length and from 0.85 to 1.8 mm. in width. The raphe runs from the apex to the basal chalaza along the dorsal sclerotesta of the central body; no flanking grooves are apparent. The elongate rectangular germination valve extends the full length of the seed and, depending on the degree of development of the wings, occupies one quarter to three quarters the width of the seed. Its surface is marked by six or seven longitudinal rows of pits about 50 μm . in diameter. At maturity the valve is reflexed, exposing the embryo cavity that extends the full length of the seed. The valve remains attached at its base to the seed. There is no obvious layer of epidermal tissue, and the structure of the inner and outer integuments has not been preserved. The genus is represented by *A. lakense* (one report) from the Lower Eocene of southern England (Chandler, 1962).

The foregoing summary of the seed characters of *Decodon*, *Mneme*, *Microdiptera*, and *Alatospermum* provides a basis for considering generic and specific delimitation. At the generic level, these distinctions can be tentatively summarized in a key, here adapted and modified from Chandler (1963b), Dorofeev (1968), and Mai and Walther (1978).

GENERIC KEY

- A. Seeds lacking dorsal grooves, germination valve remaining attached to seed body at maturity.
 - B. Seeds elongate, with lateral wings; germination valve extending full length of seed body. *Alatospermum*.
 - B. Seeds rounded, lacking lateral wings; germination valve extending one half to two thirds length of seed body. *Decodon*.
- A. Seeds with dorsal grooves, germination valve detaching completely from seed body at maturity.
 - C. Lateral wings inflated, seed body buried in wings, dorsal grooves deep; ca. 20 rows of pits on germination valve. *Mneme*.

TABLE 3. Reported species of Microdiptera.

Species	Age	Locality	Citation
<i>Microdiptera donata</i> (Holý) Tiffney	Miocene	Zittau Basin, Czechoslovakia	Holý, 1976; present paper
<i>M. elongata</i> (Dorofeev) Dorofeev	Oligocene	Kompassky Bor, W. Siberia, USSR	Dorofeev, 1963a (see also Dorofeev, 1962, 1968)
	Miocene	W. Siberia, USSR (2 localities)	Dorofeev, 1963a (see also Dorofeev, 1962, 1968)
<i>M. major</i> * Chandler	Mid Eocene	Bournemouth Freshwater Beds, England	Chandler, 1963b (but see Mai & Walther, 1978)
<i>M. parva</i> Chandler	Late Eocene	Highcliff Sands, Mudford, England	Chandler, 1963b
	Late Eocene	Lower Headon, Isle of Wight, England	Chandler, 1961b (see also Chandler, 1963b)
	Early Oligocene	Upper Headon, Isle of Wight, England	Chandler, 1963a
	Early/Mid Oligocene	Haselbach bei Dresden, E. Germany	Mai & Walther, 1978
	Mid Oligocene	Bovey Tracy, England	Chandler, 1957
	Miocene	Fasterholt, Denmark	Friis, 1980
	Miocene	Damgaard, Denmark	Friis, 1980
<i>M. tavidensis</i> Dorofeev	Mid Miocene	W. Bulgaria	Palamarev, 1971
	Mid Miocene	Hrádek, Zittau Basin, Czechoslovakia	Bůžek <i>et al.</i> , 1964
	Mid Miocene	Hartau, E. Germany	Mai, 1964
	Oligocene	Beloyarka, Transuralia, USSR	Dorofeev, 1968
<i>M. uralensis</i> (Dorofeev) Friis†	Early/Mid Miocene	Polevskoï, Ural Mts., USSR	Dorofeev, 1970 (see Friis, 1980)
<i>Microdiptera</i> sp.	Pliocene	Balkan Peninsula	Mai & Walther, 1978

*Placed in *M. parva* by Mai and Walther (1978).†Provisional usage: *nomen nudum*.

- C. Lateral wings flattened, seed body emergent from wings, dorsal grooves shallow; 5 to 10 (to 12) rows of pits on germination valve.
 *Microdiptera*.

It is clear that *Decodon* and *Alatospermum* can be separated from *Mneme* and *Microdiptera* on two good characters—ventral grooves and germination valve attachment. This negates Kirchheimer's (1935, 1957) supposition that reports of *Decodon globosus* from the Niederlausitz represented undeveloped or damaged seeds of *Mneme menzelii*; E. M. Reid (1927) clearly illustrated seeds from this locality with unattached germination valves. Further, the wings of *Alatospermum* indisputably separate it from *Decodon*.

It is far more difficult, however, to discern or defend the separation of *Microdiptera* and *Mneme*. Dorofeev (1963a) questioned the distinction between the two, and indicated in 1970 that the differences were insignificant, an opinion alluded to by Chandler (1963b). Mai and Walther (1978) unite the two genera, recognizing *Microdiptera* as a subgenus of *Mneme*. However, Friis (1980) rejects Mai and Walther's treatment and suggests that the two genera can be separated on three characters: number of pit rows on the germination valve (more than 20 in *Mneme*, 5 to 10 (to 12)) in *Microdiptera*; degree of submersion of the central body in the wing tissue (fully buried in *Mneme*, emergent in *Microdiptera*); and depth of the dorsal furrows (deep in *Mneme*, shallow in *Microdiptera*).

The stability of these characters is questionable. As noted above, some specimens identified as *Mneme menzelii* appear to have six to nine rows of pits on the germination valve. Either these are poorly illustrated or misidentified, or the character fails to hold. The degree of immersion of the central body in the wing tissue may be directly related to the degree of inflation of the wings; this seems particularly likely since many authors have mentioned that *Mneme* has thicker wings than *Microdiptera*. The variation in wing inflation and degree of emergence of the central body could be extremes of a developmental continuum. In addition, these features could be correlated with the depth of the dorsal furrows, reducing these three characters to one: the degree of development of the wings. In the present work, *Microdiptera* and *Mneme* are treated as separate genera, but only due to the absence of a first-hand, population-level investigation of the material involved. In all likelihood, Mai and Walther are correct in uniting these genera.

The preceding paragraphs involve morphological arguments for the recognition of a broad specific—and perhaps generic—concept in these genera. This conclusion is reinforced by features of the biogeography and ecology of modern-day aquatic and paludal plants. These plants commonly have very wide ranges, a fact first noted by Darwin (1859) and subsequently commented on by many authors (see Hutchinson, 1975). Indeed, Arber (1920) suggested that the range of the average aquatic plant species was greater than that of the average terrestrial species (e.g., *Potamogeton pusillus* L., *Phragmites communis* Trin.). A partial explanation for this pattern lies in the fact that bodies of fresh water are, with few exceptions, transitory in geologic time.

For this reason, successful aquatic plants must be fairly vagile, and thus capable of spreading to newly available habitats as they appear. This combination of vagility and discrete, isolated populations offers a unique situation for limited, but continuous, genetic exchange and local differentiation.

A body of fresh water offers an isolated, favorable environment to aquatic plants. A single disseminule or a small number of disseminules may become established in such a site and give rise to a large population by both sexual and asexual reproduction (Hutchinson, 1975). While the population is genetically linked to its parent source, the limited number of founding disseminules provides the opportunity for localized differentiation. Although this local differentiation may be balanced by a subsequent influx of disseminules or may be limited by the geologic duration of the water body, the entire system favors the appearance of spatially and temporally localized variants of an otherwise widespread species. In addition, while bodies of fresh water are unstable in a geologic sense, they are environmentally stable. As a result, they provide a buffered environment for growth when compared to terrestrial environments (Szafer, 1954; Hutchinson, 1975). This relative stability of environment suggests that the level of abiotic selective pressure is also relatively low. Further, this reduced level of selection pressure has probably not changed to any great degree in the last 50 million years. All of these factors argue for the stability of aquatic species over long periods of time.

It is suggested here that, in addition to a wider average range of distribution, aquatic vascular plants have a longer average species duration than terrestrial ones. This prediction can be tested in the fossil record (work in progress).

These considerations from extant aquatic plants argue for the use of a wide species concept in the identification of fossil remains of aquatics. Many of the distinctions between the various species of fossils of *Decodon*, *Microdiptera*, and (to a lesser degree) *Mneme* are not based on discrete characters, but on size and shape—characters that vary continuously. If one judges by the biological circumstances of modern aquatics, these characters cannot be seen as reliable, and it is not unreasonable to suggest that the number of species in these three genera could be reduced.

The foregoing discussion does not preface a formal revision of the three genera involved. Rather, it is intended to summarize the current state of affairs and to place the description of the Brandon material in perspective.

SYSTEMATICS

Lythraceae Jaume St.-Hil. Mém. Mus. Hist. Nat. Paris 3: 377. 1815.

Microdiptera Chandler, Bull. Brit. Mus. (Nat. Hist.) Geol. 3: 107. 1957.

Microdiptera donata (Holý) Tiffney, comb. nov.

Mneme donata Holý, Sborn. Nár. Mus. v Praze, Řada B, Přír. Vědy 32: 1–13. 1976.

Holý (1976), while acknowledging the difficulty of distinguishing *Mneme* and *Microdiptera*, assigned these specimens to the former genus on the basis

of their "lack of perfect wings." The present author has no trouble in discerning narrow wings on the illustrated specimens (Holý, 1976, *pl. 1, figs. 17-22; pl. 2, figs. 1-9*) in light of the variation seen in the Brandon material. Further, the specimens display shallow dorsal grooves ("longitudinal lateral furrows on [the] margin occasionally"), and most importantly, the germination valve has eight rows of pits. If the generic distinction between *Microdiptera* and *Mneme* is to be recognized, then these specimens clearly show closer affinities with the former genus.

Microdiptera parva Chandler, Bull. Brit. Mus. (Nat. Hist.) Geol. 3: 107. 1957. PLATES I, D-F; II, A-F; III, E-H.

Neither pollen (Traverse, 1955) nor wood (Spackman, 1949) of this family has previously been reported from the Brandon Lignite.

MATERIAL. Over 120 seeds have been collected from the silt facies of the Brandon Lignite; the seeds are common, and thousands more could be collected. The specimens are jointly assigned number 51391 of the Paleobotanical Collections of the Botanical Museum, Harvard University.

DESCRIPTION. No evidence of fruits was found. The seeds are bitegmic and anatropous. Their shape approximates that of a flattened and distorted hemisphere, the dorsal surface being flat and the ventral convex. In dorsal/ventral view the outline of the seeds varies greatly, depending upon the relative development of the wings. Elongate, angular, and smoothly rounded forms are all present (FIGURE 5). The seeds range from 0.85 to 1.3 mm. (mean, 1.02 mm.) in length and 0.6 to 1.3 mm. (mean, 0.95 mm.) in width. The raphe commences at the apex of the seed and passes along the dorsal face between the relatively deep furrows to the base, where it descends through the sclerotesta of the central body to the chalaza (PLATE II, F). The oblong, convex germination valve occupies one third to one half the

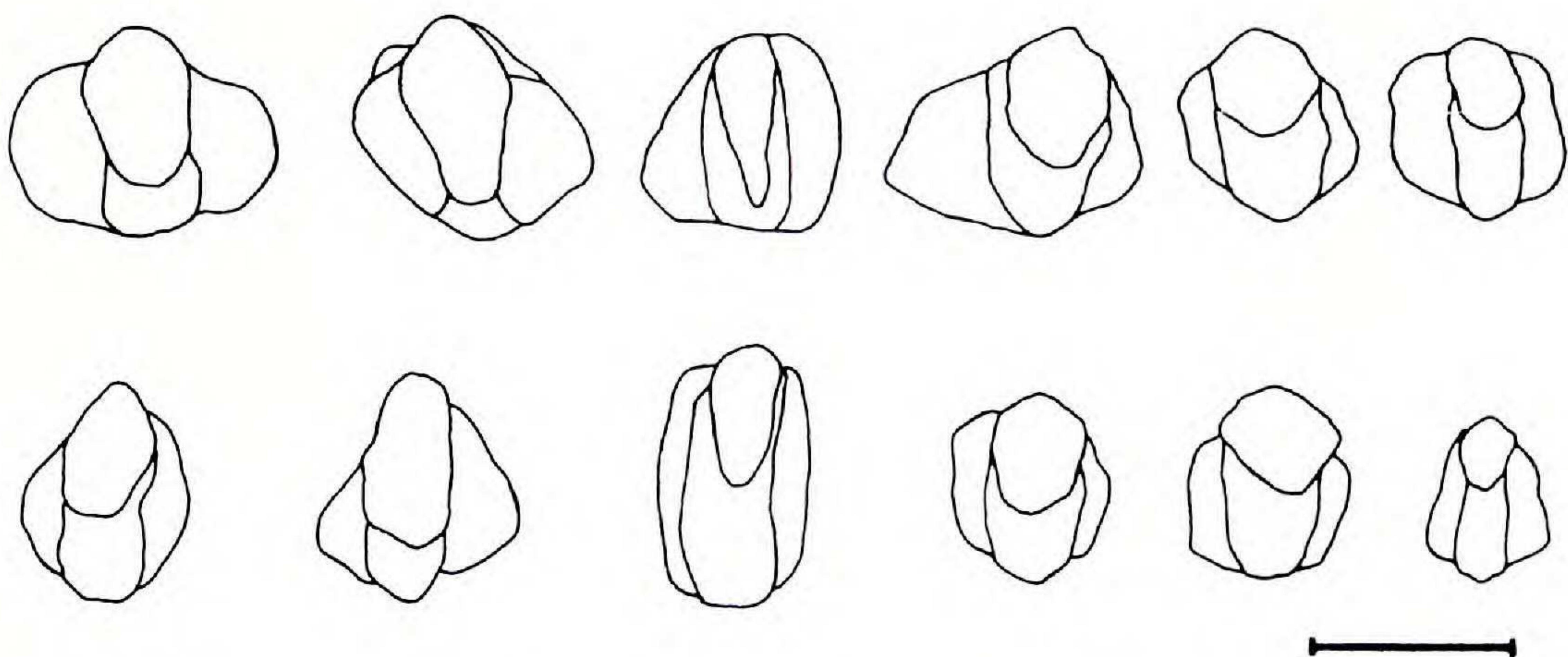


FIGURE 5. Outline drawings of *Microdiptera parva* from Brandon, demonstrating morphological variability. Ventral view, apex uppermost. Scale = 1 mm.

width of the ventral face, and one third to three quarters of its length (FIGURE 5). The surface of the valve is marked by seven to ten rows of equiaxial pits approximately 50 μm . in diameter. Upon dehiscence (PLATE II, A), the valve separates completely from the central body (PLATE II, C), splitting along a line of specialized sclereids around the margin of the valve (PLATE II, C, D). This exposes the ellipsoid embryo cavity, which extends the full length of the seed body. The epidermal tissue is not preserved. The outer integument is differentiated into two zones, one forming the central body (the inner sclerotesta), and the other a derived layer sheathing the wings (the outer sclerotesta) (PLATE III, E, F). The outer sclerotesta is frequently abraded off the surface of the wings (PLATE II, A, E) but is apparently formed of elongate sclereids. In the rare instances where this layer can be measured, it is 6–12 μm . thick and is composed of a single layer of cells. The 30–45 μm . thick inner sclerotesta sheathes the embryo cavity in one to three layers of cells that measure approximately 28×12 – $18 \mu\text{m}$. In the vicinity of the germination valve, this layer thickens to 50–90 μm . and is formed of sclereids that commonly have angular lumina indicative of the presence of crystals (PLATE III, H). The spongy mesophyll between the inner and outer sclerotestae is restricted to the two wings and is composed of roughly isodiametric parenchyma cells 12–18 μm . in diameter (PLATES II, E; III, E, F). The inner integument is poorly preserved but consists of a single layer of narrow, elongate (3 – $5 \times 40 \mu\text{m}$.) cells (PLATE III, H).

AFFINITIES. The morphology of these seeds is in complete agreement with that of *Microdiptera* and falls within the range of *M. parva*. In light of the ecological/biogeographic observations on aquatics presented earlier, no reason is seen to erect a new species for this first North American report.

ECOLOGY. *Decodon*, *Microdiptera*, and *Mneme* tend to occur together at many European localities. P. A. Nikitin (1929) initially suggested that *Mneme* was usually found in the absence of *Decodon* in certain Siberian deposits, from which he concluded that the two genera were ecologically distinct. This appears to have been a function of the sample since a statistical examination of the 75 floras that bear *Mneme*, *Decodon*, and *Microdiptera* reveals that there is no significant negative correlation between any combination of the three genera. In general, all three are associated in the fossil record with communities and depositional environments derived from swamp or lakeside habitats, rather than from more mesic upland sites. An excellent example of this is found in Holý's study of the Miocene of Hrádek nad Nisou, Czechoslovakia (1975, 1976). The clear taxonomic and taphonomic association of the three genera suggests that extant *Decodon* may be taken as a common ecological model.

Decodon verticillatus is a deciduous perennial shrub of the margins of swamps, ponds, and streams from Nova Scotia, southwestern Quebec, and southern Ontario, south to Florida and eastern Texas (Correll & Correll, 1972; Graham, 1975). The seeds apparently germinate on banks; the branches of the resulting plant are weak and soon fall over (Sculthorpe, 1967; Hutchinson, 1975). If they fall into water, aerenchymatous tissue and roots are developed, leading to the formation of a mat. Leaf-bearing shoots arise from this mat,

ultimately to collapse and repeat the process. As a result, the plant achieves rapid vegetative spread, forming dense mats along waterways (Correll & Correll, 1972). The flowers are entomophilous (Hutchinson, 1975), although reduced flower size may presage a shift to self-pollination (Sculthorpe, 1967). The plant is higher in alkaloids than are most aquatics, perhaps as a result of its relative accessibility to herbivores (Hutchinson, 1975). *Decodon* is known to be transported both internally and externally by waterfowl (Ridley, 1930).

DISCUSSION

The discovery of *Microdiptera* at Brandon adds another genus to a growing list of taxa present in the Tertiary floras of both eastern North America and Europe, including *Magnolia* L. (Tiffney, 1977), an undescribed Brandon fruit similar to *Rehderodendron* Hu, and a recently discovered occurrence of *Wetherellia* Reid & Chandler and *Palaeowetherellia* Chandler from the Eocene of Virginia and Maryland (research in progress). This pattern is presumably a holdover from an early Tertiary floristic exchange across the North Atlantic (Tiffney, 1980b). *Decodon* provides a modern counterpoint to this pattern, having been widely distributed in the European Tertiary but presently persisting only in eastern North America. Presumably *Decodon* and *Microdiptera* coexisted in the North American Tertiary, but only *Decodon* survived the Quaternary.

A concluding speculative remark on phylogeny: the earliest of the four related genera is *Alatospermum*, which has the characters of both *Decodon* and *Microdiptera*/*Mneme*. *Alatospermum* could thus be considered as ancestral to the other three genera, giving rise to the *Decodon* morphology in the Late Eocene through suppression of the wing tissue, and to *Microdiptera* in the Late Eocene through complete detachment of the germination valve. *Mneme* could have been derived from *Microdiptera* in the Oligocene by very **minor developmental changes**.

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PEABODY MUSEUM AND DEPARTMENT OF BIOLOGY
YALE UNIVERSITY
Box 6666
NEW HAVEN, CONNECTICUT 06511

EXPLANATION OF PLATES

PLATE I

FIGURES A–C. Seeds of *Decodon verticillatus*, covered by cuticle. A, dorsal view, apex down (*Rehder 1297*). B, apical/dorsal view: hilum a clear circular hole; micropyle ventral to it, less well defined. C, ventral view, apex up: separation between weakly developed lateral wings and central body can be seen; germination valve in upper half of central body.

FIGURES D–F. Seeds of *Microdiptera parva* from Brandon. D, seed of average shape, ventral view, apex down. E, semi-elongate seed, ventral view, apex to left: cellular depressions on germination valve distinct. F, seed with unequally developed wings, central body displaced to one side, ventral view, apex down. Scales = 100 μ m.

PLATE II

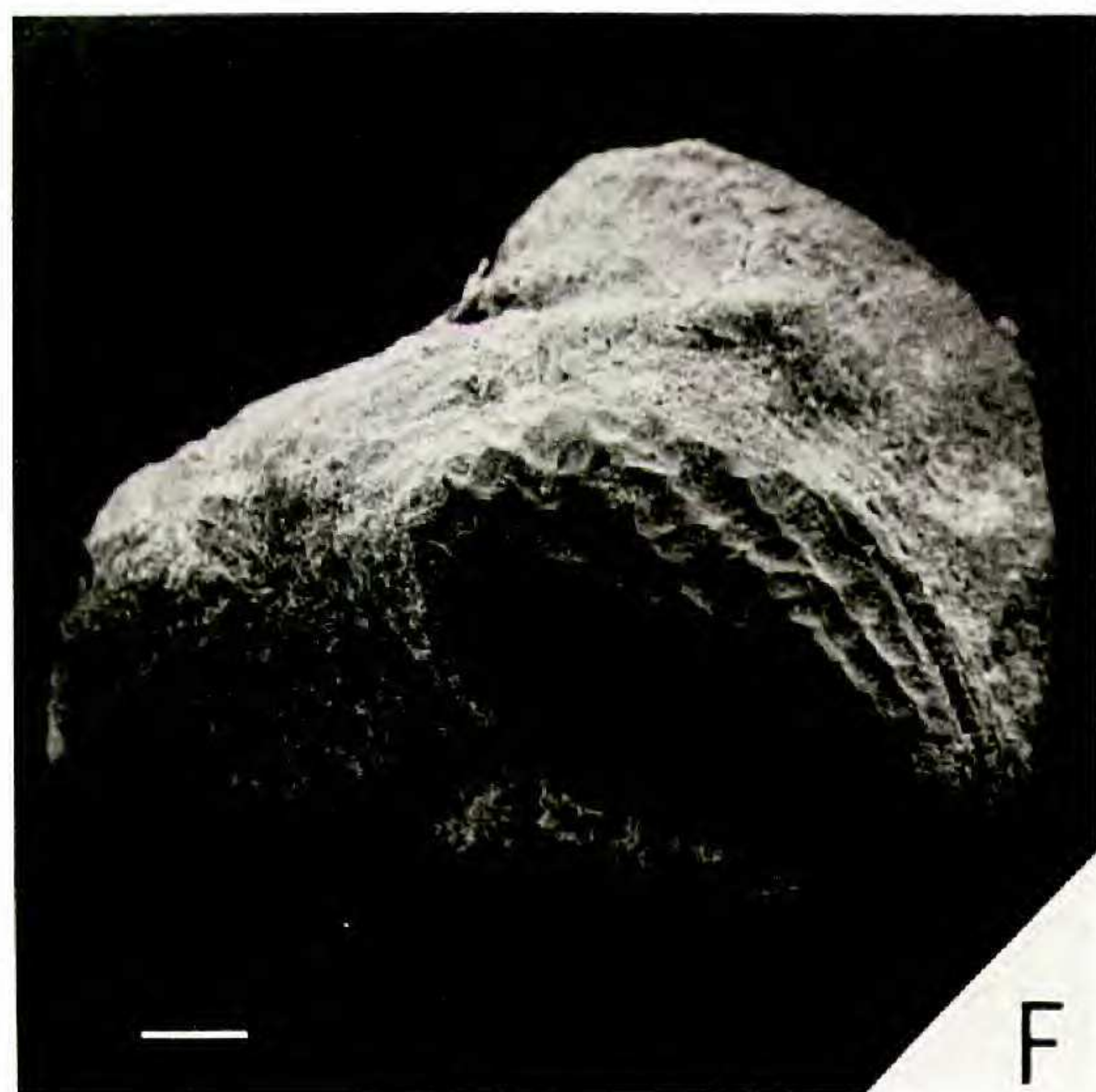
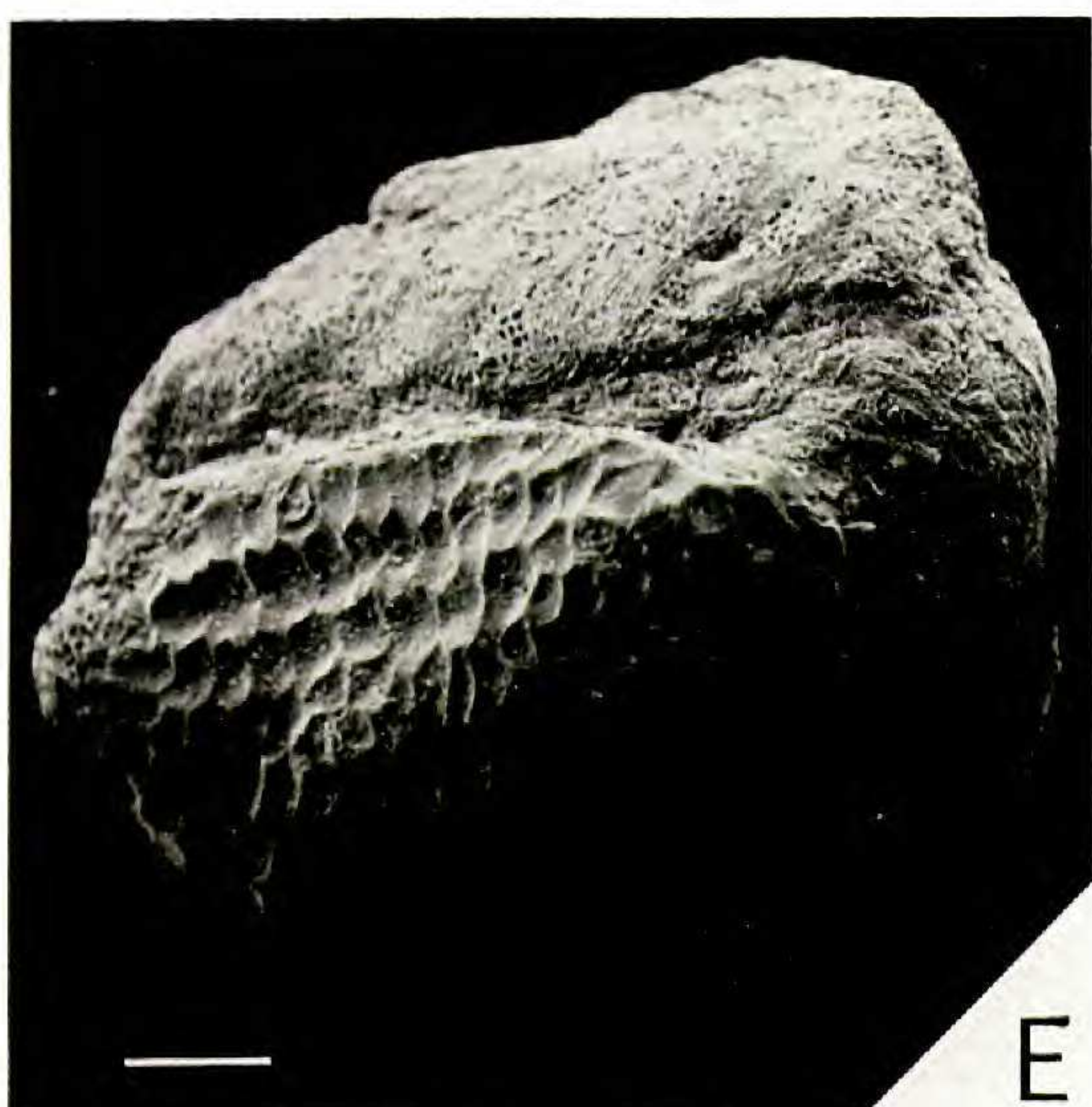
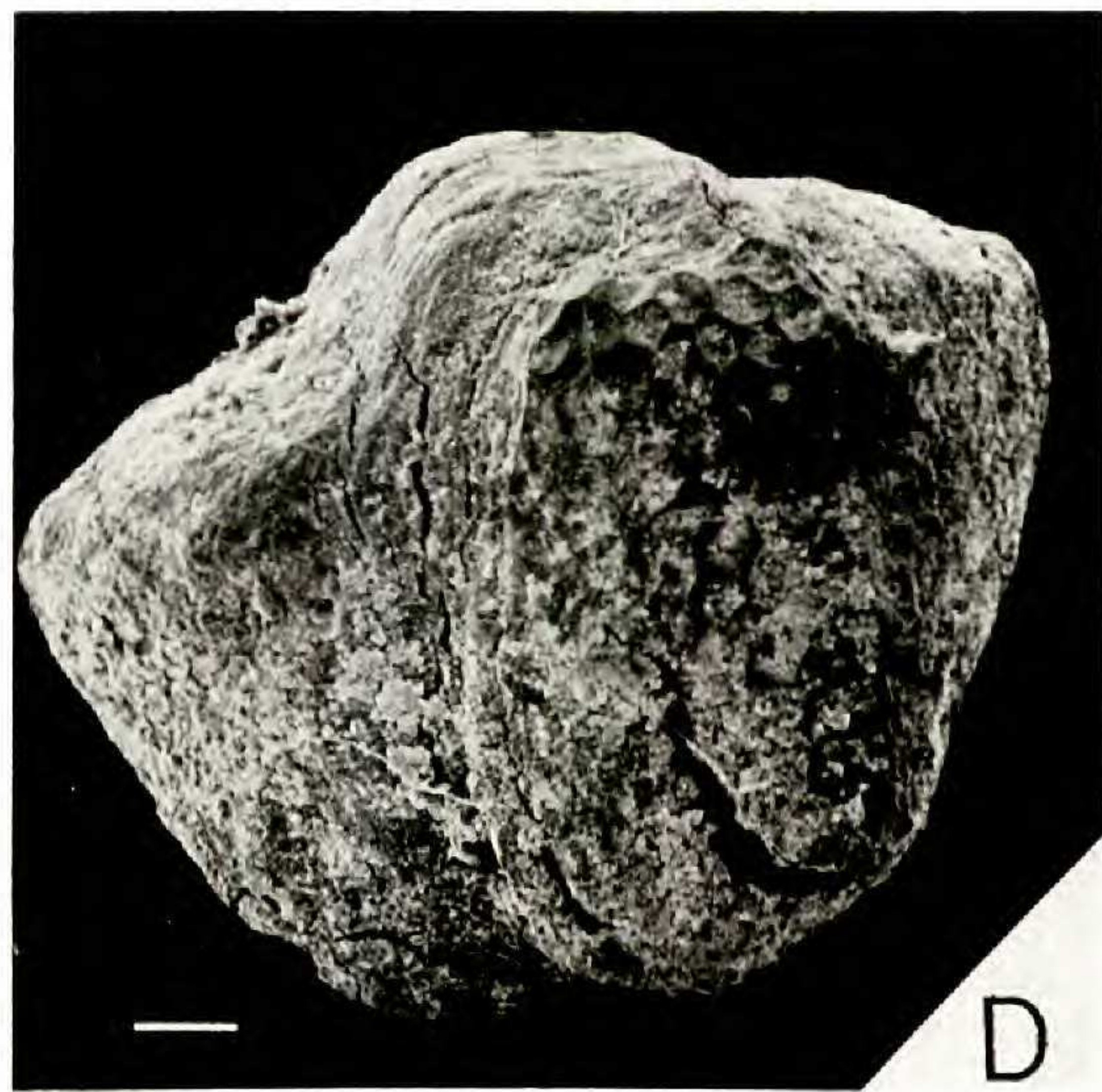
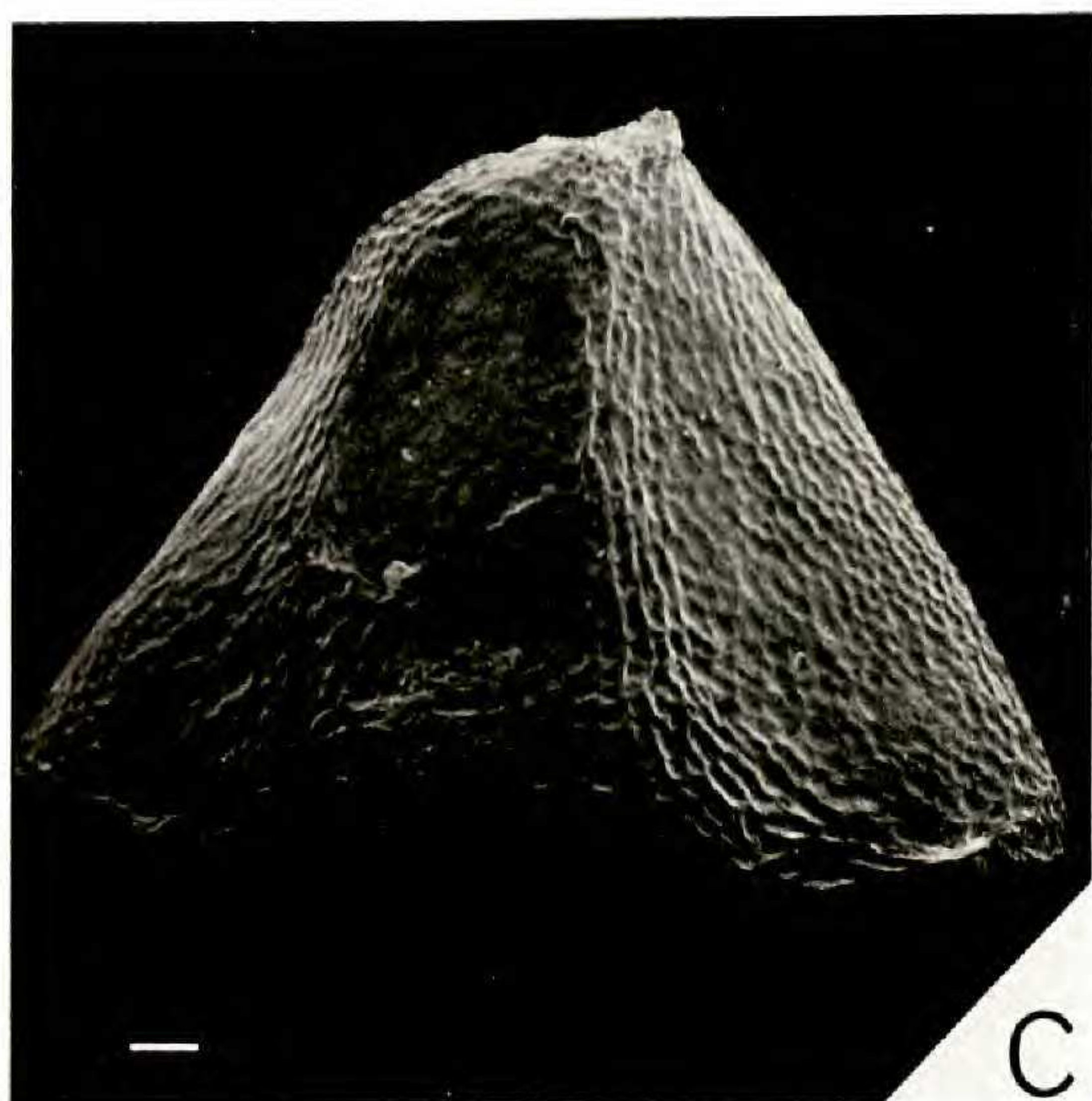
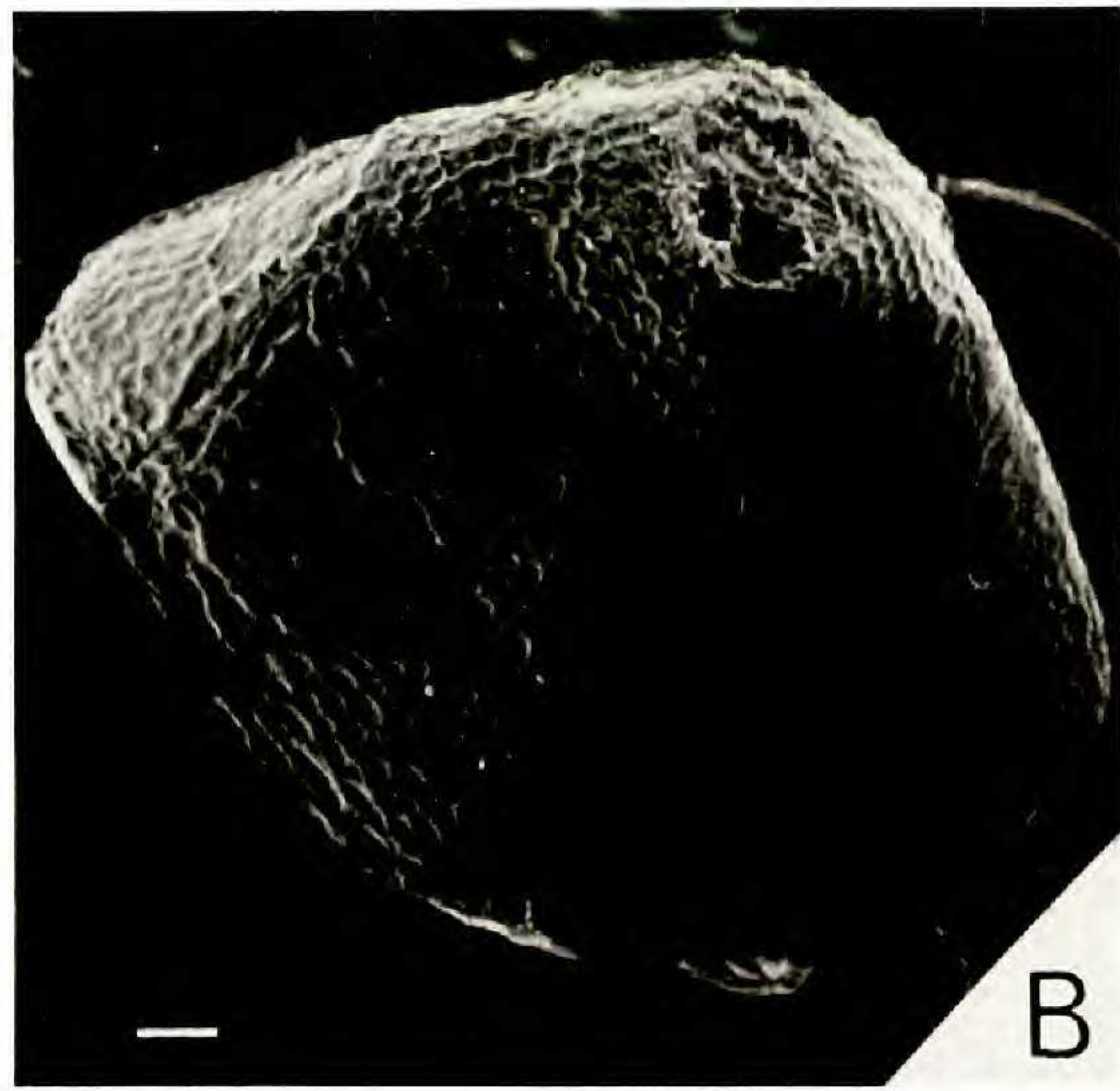
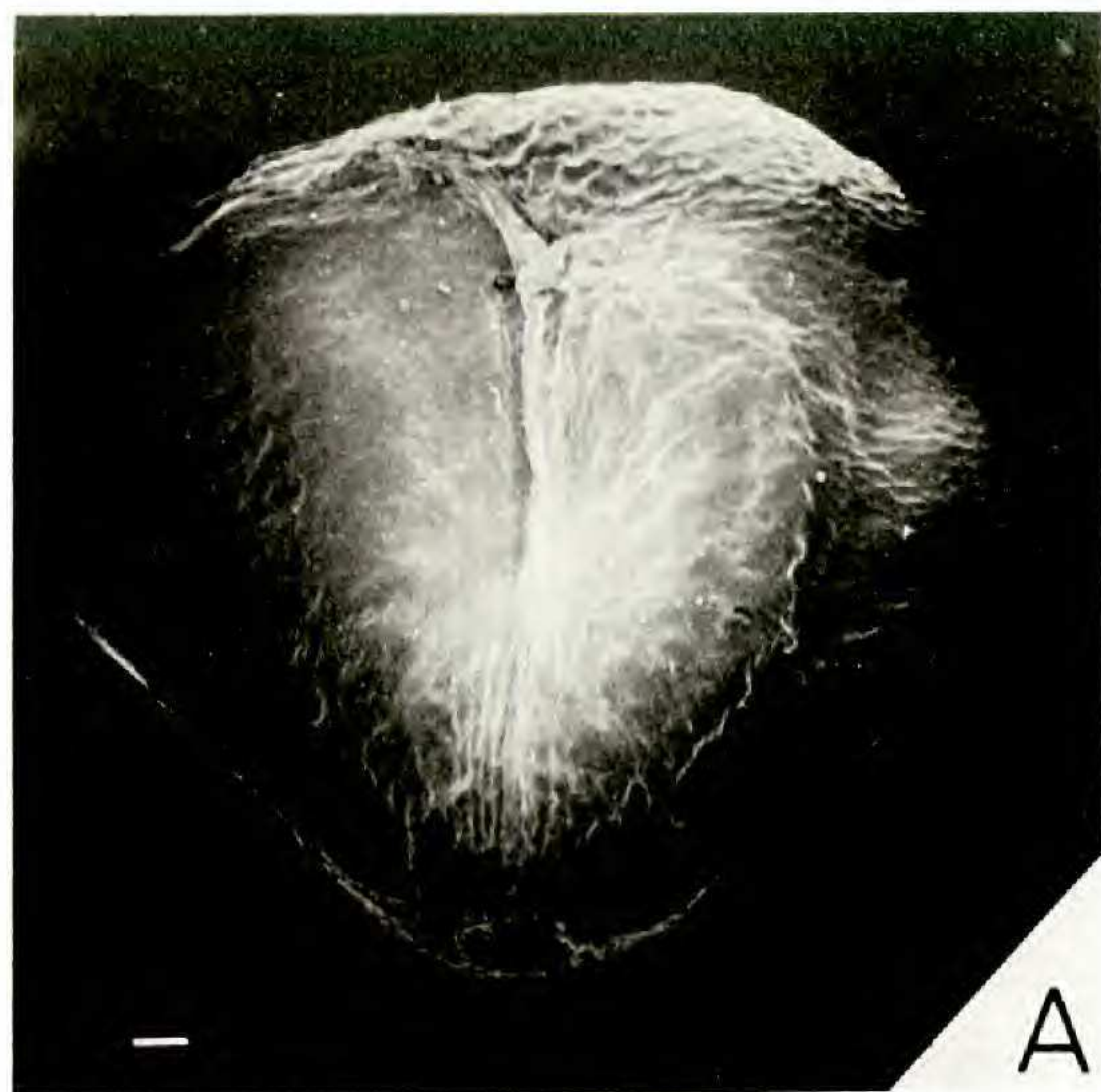
FIGURES A–F. Seeds of *Microdiptera parva* from Brandon. A, lateral view, apex to right: germination valve starting to dehisce (note striations on outer surface of central body and their absence due to abrasion on near wing, exposing underlying spongy cells). B, ventral germination valve, apex to right. C, apical/ventral view: germination valve lost, exposing embryo cavity (ringed by cells of marginal zone of dehiscence). D, detail of dehiscence zone, apical view: embryo cavity to right, exterior to left. E, detail of outer ventral surface, apex to left: elongate elements of outer sclerotesta clear on central body and in some places on wing; cells of spongy mesophyll (exposed by abrasion) to lower right. F, dorsal view, apex to left: two dorsal furrows flanking path of raphe, which runs from apical hilum to small, subbasal depression leading to chalaza. Scales = 100 μm . in A–C, E, F; 10 μm . in D.

PLATE III

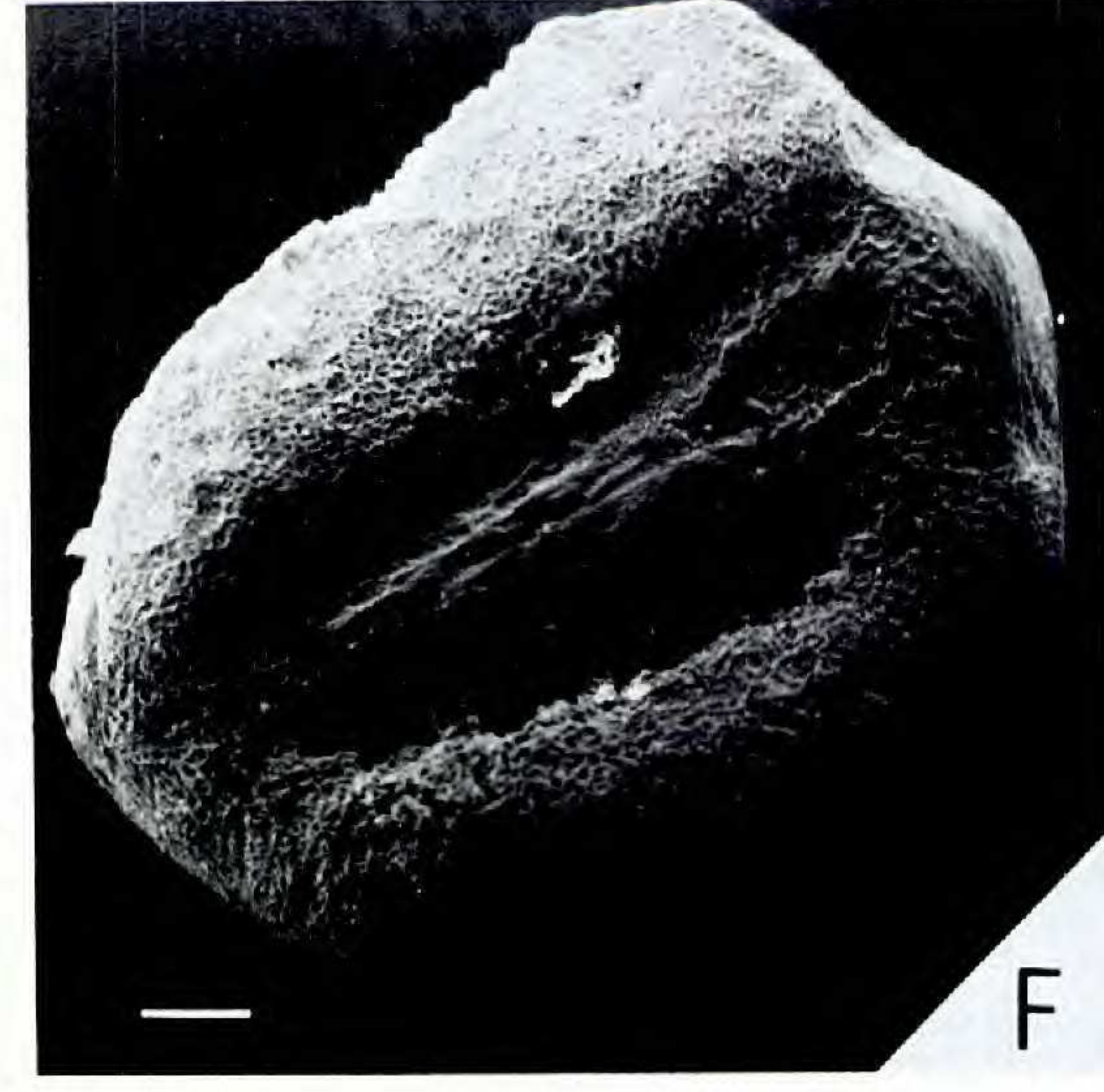
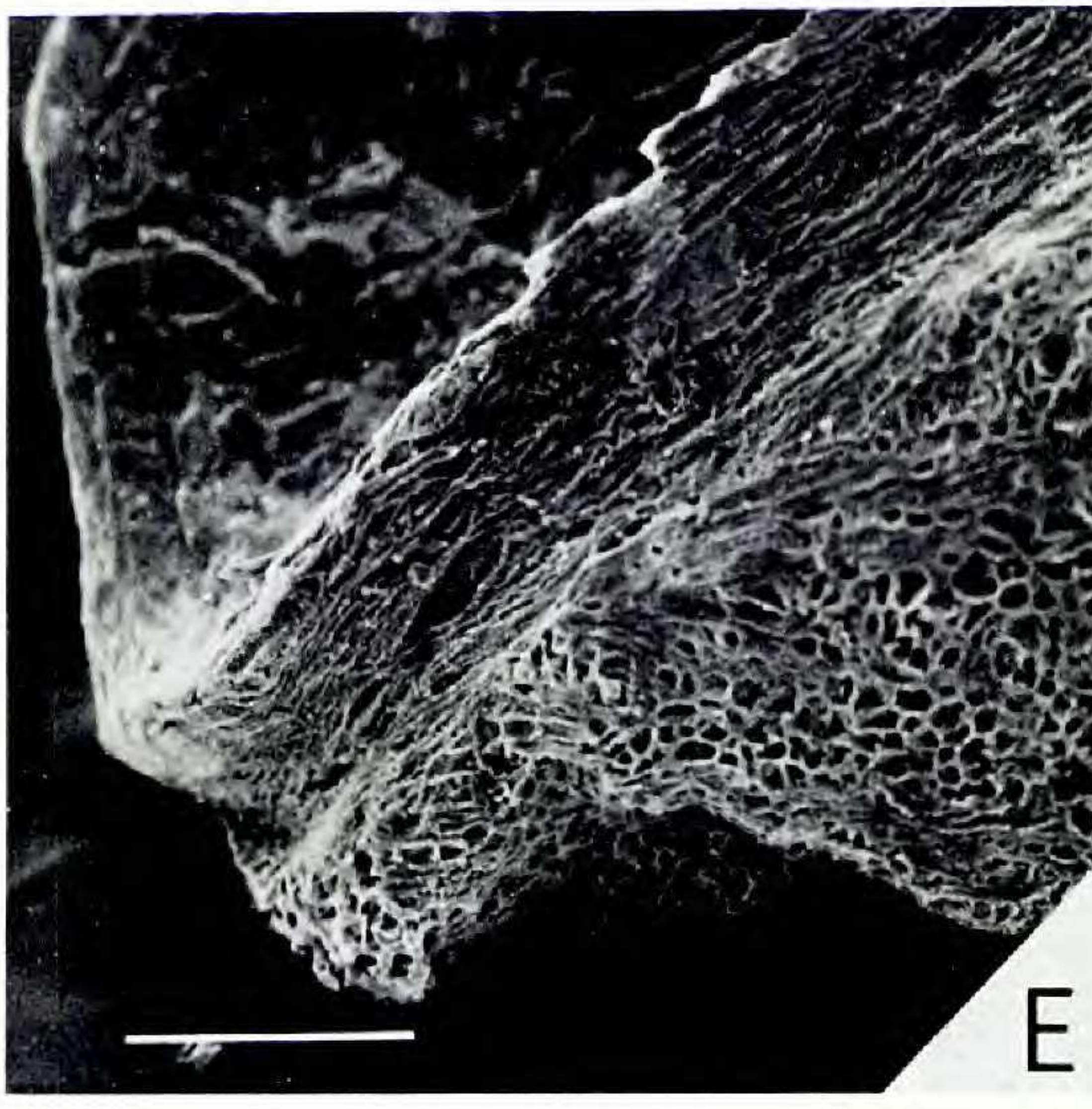
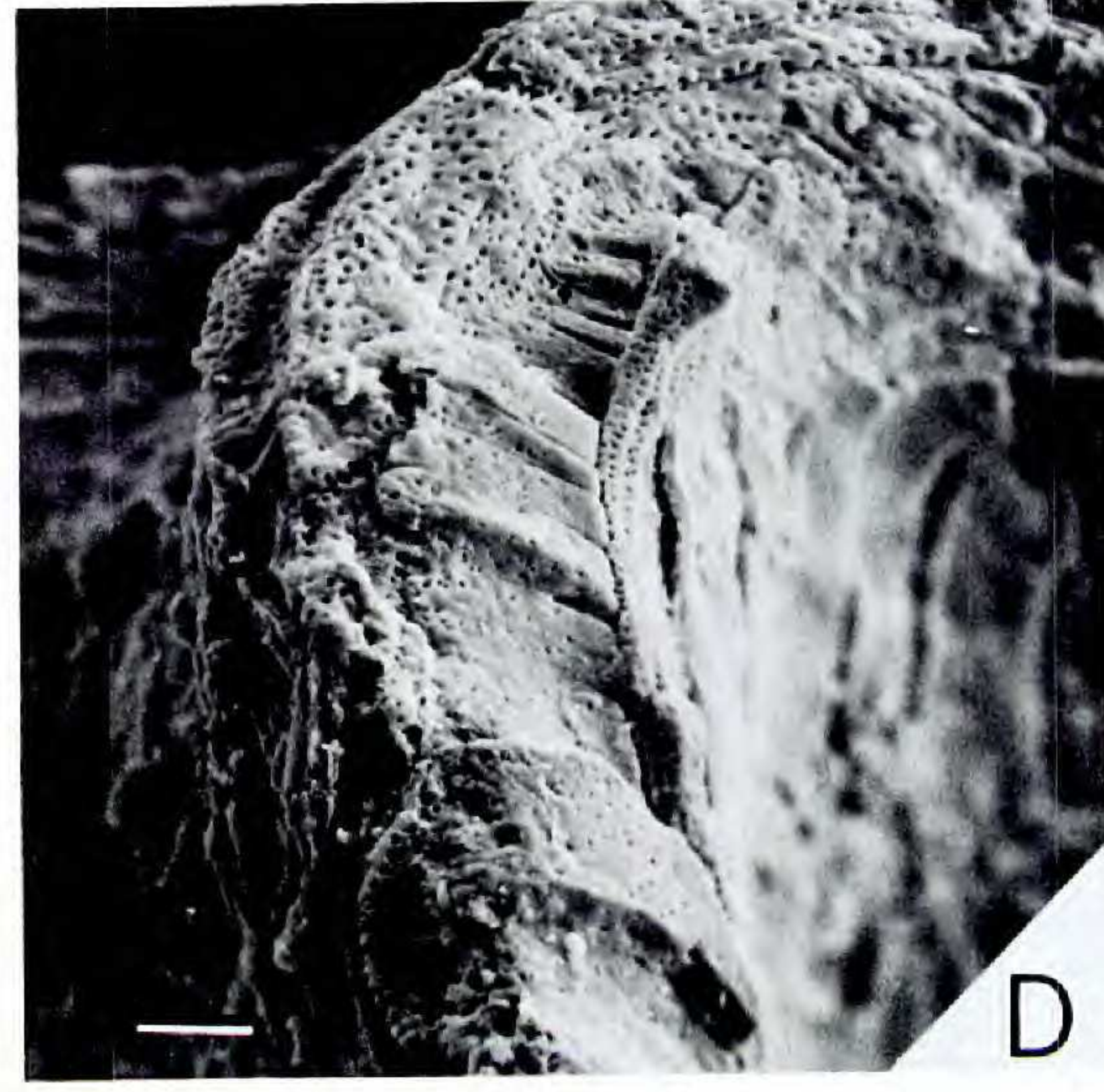
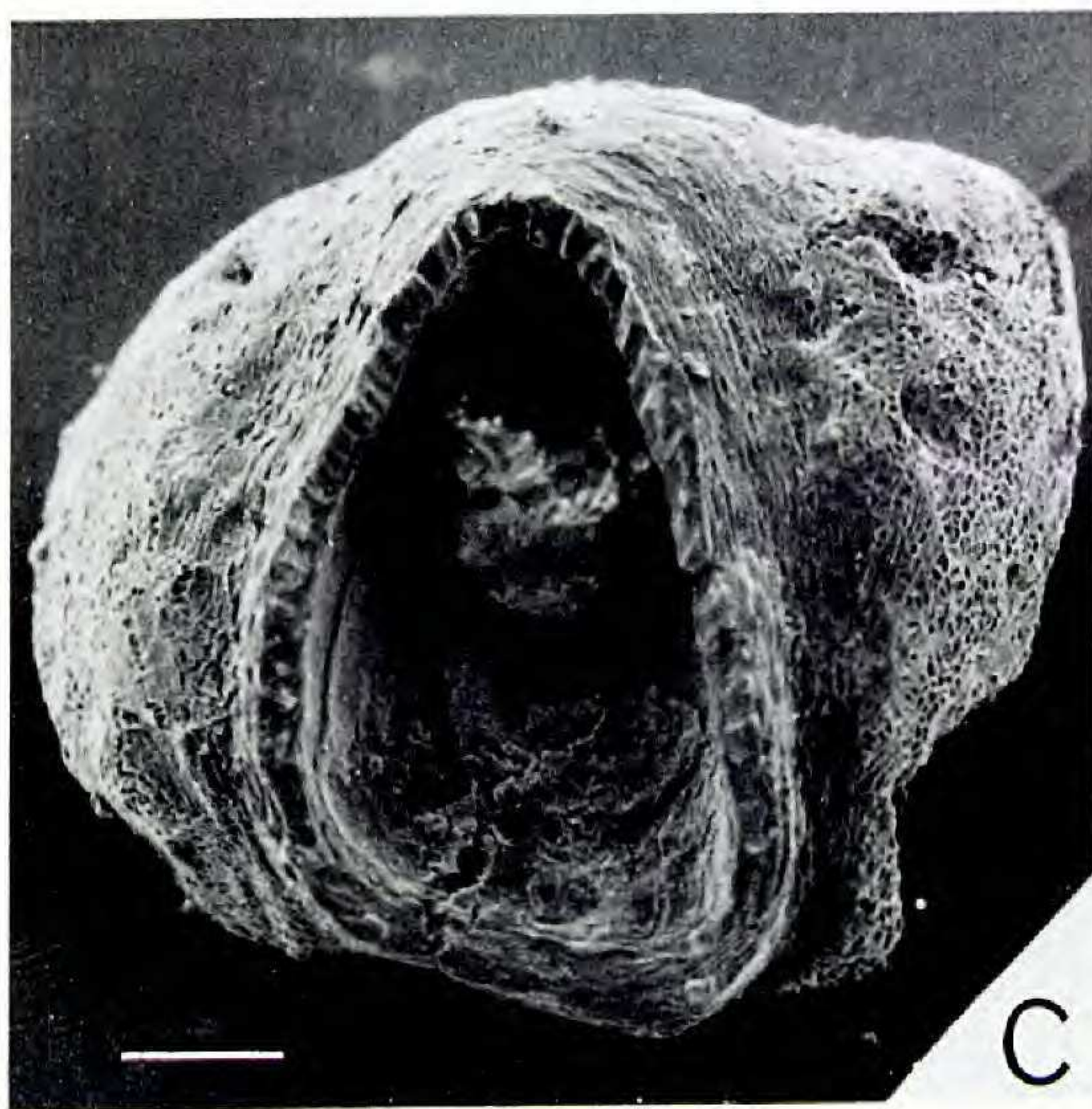
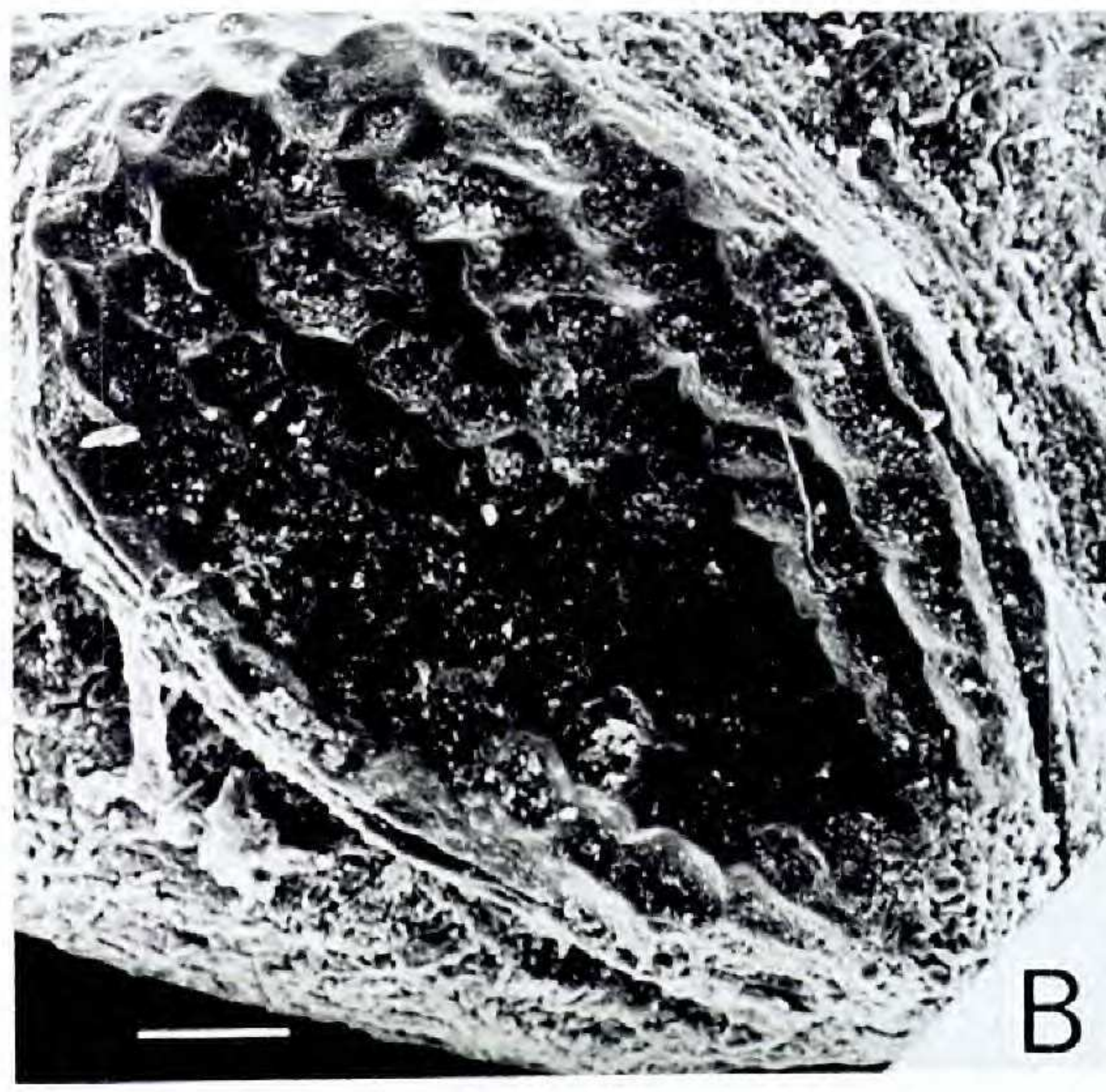
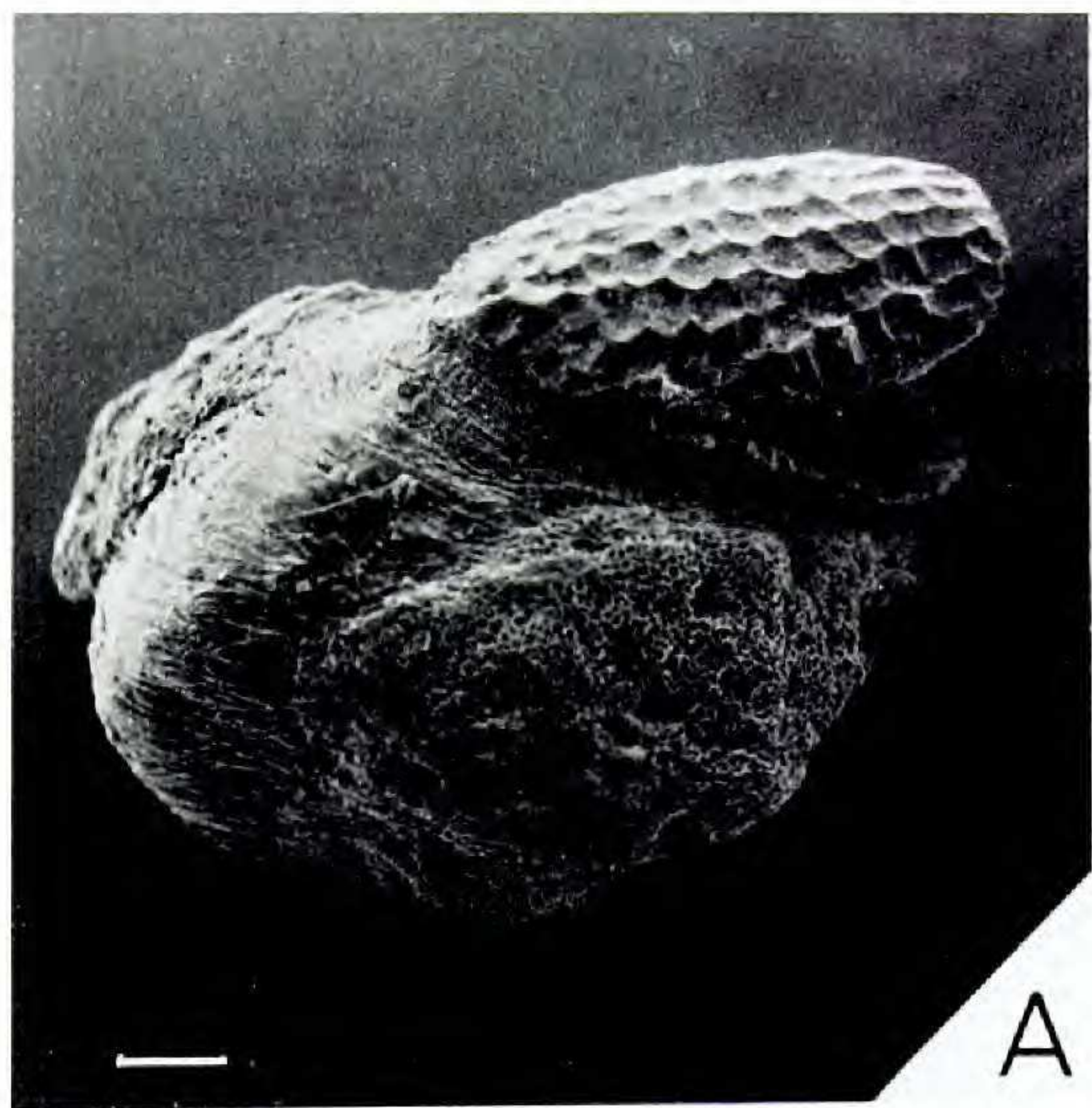
FIGURES A–C. *Mneme menzelii* from Frecheu, Germany (Miocene): A, ventral view, $\times 1.7$, apex down; B, dorsal view, $\times 1.7$, apex down, showing two dorsal furrows; C, cross section, $\times 542$, embryo cavity to left (note thick inner sclerotesta and thin outer).

FIGURE D. *Decodon verticillatus* (Rehder 1297), cross section, $\times 37$, ventral side up (note thin external sclerotesta and thick inner).

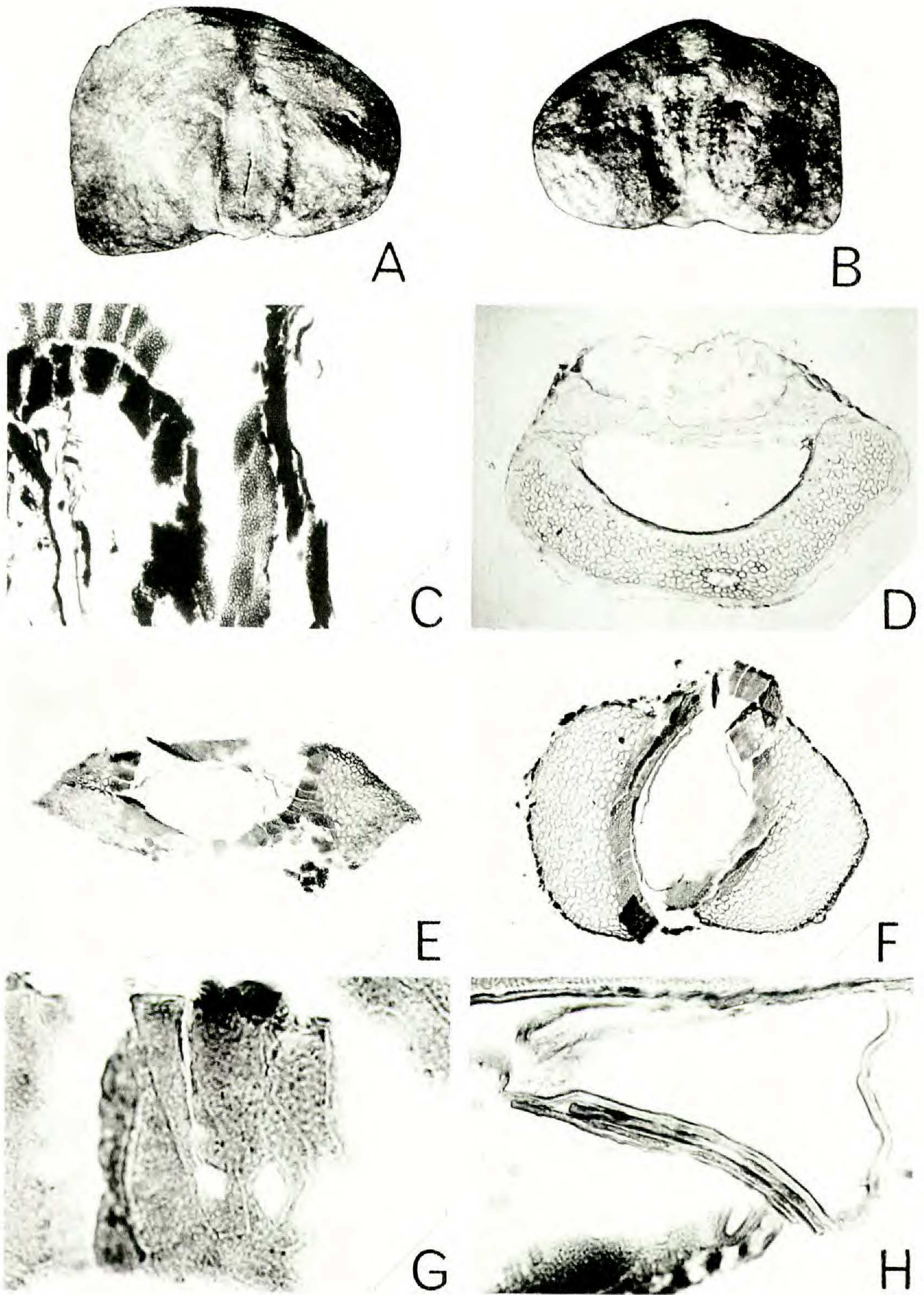
FIGURES E–H. *Microdiptera parva* from Brandon: E, cross section, $\times 66$, ventral side up (note thin outer sclerotesta, thick inner sclerotesta, and spongy tissue of wings); F, longitudinal section, $\times 66$, apex up, well-developed wings clearly evident; G, inner integument cells, $\times 490$; H, detail of inner sclerotesta beneath germination valve, $\times 490$, showing angular sclereid lumina indicative of crystal inclusions.



TIFFNEY, BRANDON LIGNITE, VI



TIFFNEY, BRANDON LIGNITE, VI



TIFFNEY, BRANDON LIGNITE, VI